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Species-oriented model approaches to *Daphnia* spp.: linking the individual level to the population level

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1 General introduction

The genus *Daphnia* is a widespread inhabitant of standing freshwaters from the arctic to the tropics (FERNANDO *et al.*, 1987; HANEY & BUCHANAN, 1987; HRBÁČEK, 1987). Its occurrence has been reported for various trophic states ranging from oligotrophic to eutrophic systems and for a broad range in habitat size and morphology spanning from small ponds and shallow lakes to the pelagic zone of large, stratified lakes and reservoirs (KASPRZAK & SCHWABE, 1986; BENNDORF, 1990; FLÖSSNER, 2000; HORN, 2003; JEPPESEN *et al.*, 2004). In the majority of these limnetic systems, zooplankton communities can be dominated by daphnids in terms of abundance and biomass — at least during certain time intervals of the vegetation period. Thus, *Daphnia* has a great importance within lake food webs and it has been pointed out that *Daphnia* is a key species for pelagic systems (STERNER, 1989; CARPENTER & KITCHELL, 1993). In comparison to other zooplankters, daphnids can reach high filtration rates (MUCK & LAMPERT, 1984; REYNOLDS, 1984) and potentially remove particles over a broad range of sizes from roughly 0.5 to 50 μm (BURNS, 1968; GELLER & MÜLLER, 1981; REYNOLDS, 1984). Therefore, zooplankton community grazing rates are often dominated by *Daphnia* (THOMPSON *et al.*, 1982). In temperate lakes, grazing by daphnids commonly leads to a pronounced clear water phase and daphnids are generally believed to be important in structuring phytoplankton communities and phytoplankton succession over the year (LAMPERT *et al.*, 1986; SOMMER *et al.*, 1986; HORN, 1991). If conditions are convenient, *Daphnia* can realize effective filtration rates of more than 1 d^{-1} indicating that the whole water body is filtered at least once per day (THOMPSON *et al.*, 1982; KÖTHE & BENNDORF, 1994). In conclusion, due to its significant role in aquatic food webs the genus *Daphnia* appears to be important in both scientific as well as applied issues in limnology.

Moreover, *Daphnia* is a frequently studied organism in general ecology, which has been "used on nearly every level of biological investigation" (original citation from DE BERNARDI & PETERS, 1987). The study of MCCAULEY & MURDOCH

(1987) introduced *Daphnia* as a paradigm for basic concepts in ecological theory, in particular for those concepts related to species interactions and population dynamics. Daphnids are easy to cultivate and handling of animals is unproblematic, which is mirrored by a long tradition of more than 100 years of research on *Daphnia* in experimental biology (EDMONDSON, 1987). Finally, due to its well studied biology and an enormous number of empirical investigations on the ecology of *Daphnia*, this genus became an important model organism in theoretical ecology and modelling studies. Nowadays, we know for almost all issues in theoretical ecology examples for an application to daphnids and several recent developments of conceptual frameworks in ecological modelling have been pioneered on the genus *Daphnia* (e.g. KOOIJMAN & METZ, 1984; NISBET *et al.*, 1989; DE ROOS *et al.*, 1992; MOOIJ & BOERSMA, 1996; ANDERSON *et al.*, 2005).

On the other hand, the attracting properties of *Daphnia* for researchers have also led to a diversification of research conducted and to bring these findings into context is a complex task. One useful strategy to realize a synthesis of current knowledge is the application of mathematical models that enable scientists to investigate the outcome (net effect) of several interacting processes on a higher organizational level of the respective system. In fact, an overwhelming number of ecological models focusing on diverse topics of the ecology of *Daphnia* has been published in the last decades (e.g. SINKO & STREIFER, 1969; PETERS & RIGLER, 1973; GABRIEL, 1982; MCCAULEY *et al.*, 1990b; ANDERSON *et al.*, 2005). However, most of these investigations employed their own specific model approach, which is designed for a single, well-defined problem (problem oriented modelling). Consequently, it is difficult to link such problem-oriented approaches to each other or to realize a cross-validation of different models. Furthermore, still many models are predominantly evaluated in a rather qualitative manner and often lack a comprehensive model validation. But such a thorough model validation is strongly demanded in applied sciences, where the model outputs are used in decision support systems or for prognostic purposes. In consequence, many models from basic ecology cannot easily be adapted to applied purposes.

It is astonishing to note that we still lack a prototype-like model framework for the important genus *Daphnia* that covers basic aspects of the biology of *Daphnia*[1] and produces quantitatively sound outputs. Such a model prototype has the potential

[1] e.g. life-cycle, resource-dependent growth, temperature dependence

to provide a unifying platform for scientists working on different kinds of *Daphnia* models. But it could also act as a starting point for further applications in scientific work related to *Daphnia* by providing a mechanistical and thoroughly validated set of model equations and parameters. An powerful example how prototype-like, thoroughly validated model approaches promote further research is given by the work on fish bioenergetics by HANSON *et al.* (1997). They developed a properly validated energy allocation model of different fish species, that calculates growth and reproduction on basis of consumption data. As an innovative addition to the scientific work of model development they furthermore implemented their model as a standard user software (Fish Bioenergetics 3.0) that enables other scientists to use this model for their own purposes. As a consequence, fish bioenergetics is nowadays a widespread model software that is used by many studies in fisheries for back-calculations of food consumption on basis of growth data of fish (e.g. HELMINEN *et al.*, 1990; WORISCHKA & MEHNER, 1998; PENCZAK *et al.*, 2002; HÖLKER & HAERTEL, 2004). Moreover, other scientists started to contribute to this software by adding parameter sets for further fish species (e.g. RUDSTAM *et al.*, 1994; TOLONEN, 1999) or even invertebrate taxa (BRYLAWSKI & MILLER, 2003).

This thesis, therefore, is focused on the development of a comprehensive model framework of *Daphnia* that spreads over different levels of biological organization and provides several interfaces for potential applications in other studies. Outputs of the model system will be validated on independent data in order to prove its quantitative correctness. It should enable applications in theoretical ecology, in experimental studies demanding a theoretical background as well as in applied issues. This corresponds to a 'species-oriented' approach. An important feature of the intended model system will be a nested design of its compartments.

From one point of view the application of 'problem-oriented' models is still reasonable, since it is generally recommended to keep models as simple as possible and general systems theory demands a defined system with distinct system boundaries. Also, the level of complexity chosen for a given modelling effort should be based on the goals of the study. This is of especial importance for modelling in environmental sciences due to the high complexity of these systems (e.g. RAUCH *et al.*, 1998). The focus on a specified problem helps the investigator to cope with the systems complexity in a practical manner. Nevertheless, RAUCH *et al.* (1998) also pointed out that it is hard to couple existing models, whose structure are not consistent to each other. Still

from another point of view one can ask how such a diversity of problem-oriented models of an organism could promote a unifying view on the biology of this organism? A problem-oriented approach implies that reutilization of existing model compartments is scarce and thus avoids cross-validation of the competing models. In this respect it appears a promising intention to develop a nested 'species-oriented' model that acts as a starting point for specific, problem-oriented model applications. Due to the nested character of the framework users not necessarily have to apply the complete system but just select the parts of interest. Such a system would also be open for modification and extension by other scientists and thus could potentially act as an integrating platform for researchers working on this species. Due to the central role of *Daphnia* in limnology and general ecology and the overwhelming empirical knowledge available, it would be an appropriate model organism for such a species-oriented modelling effort.

Many approaches to individual or population level dynamics of *Daphnia* apply models that account for resource-dependent growth and temperature (e.g. WULFF, 1980; NORBERG & DEANGELIS, 1997). Evidently, temperature as well as food conditions are important factors for the observed dynamics, which are well documented by empirical investigations (VIJVERBERG, 1976, 1980; LYNCH *et al.*, 1986; URABE & WATANABE, 1990). Moreover, these two environmental factors played a great role in classical experiments on basic growth kinetics and, also, in the theory of competition (e.g. BURNS, 1969; TILMAN, 1982; FORAN, 1986; ROTHHAUPT, 1990). However, in the last decades several investigations documented complex processes effecting the population dynamics of *Daphnia* apart from resource availability and temperature. Already in 1954, SLOBODKIN discovered in a classical mesocosm experiment that the demography of *Daphnia obtusa* showed large fluctuations during its development. The reasoning was rather straightforward: delaying effects were responsible for the fluctuations, e.g. because of time needed for eggs to develop or for juveniles to become adult or due to starvation induced effects. An equilibrium of the population was only possible if the population demography shows a dynamic equilibrium, as well. In fact, the growth characteristics of a population strongly depend on the populations demography and recent field studies documented fluctuating demography and its consequences for *Daphnia* populations (e.g. MATVEEV & GABRIEL, 1994; HÜLSMANN, 2003). They found that observed population dynamics cannot be understood without taking these demographic effects into account (see also WAGNER *et al.*, 2004).

Another fact increasing the complexity of observed population dynamics of *Daphnia* is the size-dependence of top-down acting processes. Predation on *Daphnia* often acts size-selectively; whereas fish feeds selectively on larger individuals, invertebrate predators like *Chaoborus* or *Leptodora* do prefer smaller prey (HALL *et al.*, 1976; LYNCH, 1979; LAZZARO, 1987). These different predation regimes strongly affect population growth rate (MOOIJ *et al.*, 1997), which would be even more dramatic if predation turns out to be selective for egg-bearing females (TUCKER & WOOLPY, 1984). *Daphnia*, however, can cope with these different predation regimes by adjusting their life-history in order to weaken the predation effects (STIBOR, 1992; RIESSEN, 1999; RINKE *et al.*, 2005). Indeed, such life-history adaptations have been documented in field studies (HÜLSMANN, 2001). Finally, recent studies provided evidence that besides food quantity also food quality can be an important limiting factor for *Daphnia*. Main determinants of food quality are stochiometric composition and the amount of essential fatty acids (DEMOTT & MÜLLER-NAVARRA, 1997; GULATI & DEMOTT, 1997; HESSEN *et al.*, 2005).

In conclusion, a 'species-oriented' model framework of *Daphnia* needs to cover several levels of biological organization in order to account for such a diversity of interacting processes. It explicitly appears that individual level characteristics are interacting with population level dynamics, e.g. in terms of size-selective predation or demographic effects. Additionally, physiological processes are relevant and need to be regarded in a detailed fashion. The latter would be necessary to account for food quality effects or for a mechanistic description of life-history plasticity, which is viewed to be associated with a plasticity of underlying energy allocation patterns. The tight interactions between individual and population level characteristics have already been recognized by KAISER (1979) who pioneered an individual-based methodology to model the dynamics of a population (individual-based paradigm, see GRIMM, 1999). These 'individual-based models' (DEANGELIS & ROSE, 1992; GRIMM, 1999) allow to account for individual behavior and properties and, as well, for their variability within the population. Individual-based models were also proven to provide an excellent methodology for modelling population dynamics of *Daphnia* (GABRIEL, 1982; KOOIJMAN & METZ, 1984; RATTE, 1996; FIKSEN, 1997; MOOIJ *et al.*, 2003). However, existing approaches are strictly 'problem-oriented' and reutilization of distinct model compartments is unusual. This is surprising since, for example, all these models cited above included a model compartment for growth and reproduction of *Daphnia*.

Another problem that might appear in individual based models is their high computational demand making them sometimes hardly applicable for community level models (e.g. in water quality management models). An alternative to individual-based models are recently developed physiologically structured population models (DE ROOS & PERSSON, 2001). They also allow the inclusion of individual level characteristics but provide a more efficient simulation of population dynamics.

The aim of this study is to develop a species-oriented model for the simulation of *Daphnia* that provides the necessary complexity to account for demographic effects, life-cycle characteristics and physiological properties on the one hand and that allows an efficient simulation on the population level on the other hand. As a first step, recent developments in zooplankton modelling were reviewed and problems of existing approaches evaluated (see chapter 2). Special emphasis is put on community level models commonly employed in applied limnology (water quality management models). Such models include different trophic levels and several direct and indirect relationships between their state variables. They require an efficient simulation due to the complexity of their structure but also claim a realistic quantitative output. Besides their application in applied limnology water quality models are believed to provide a suitable tool for an integrating view on lake ecosystems (PETZOLDT & SIEMENS, 2002). The content of chapter 2 should enable an identification of the basic requirements of a species-oriented model approach of *Daphnia*. In the third chapter (see chapter 3), empirical knowledge is used to develop an individual level model of *Daphnia* that will be applied in an individual based simulation in order to gain information from the population level. Although purely empirical, the model already allows to combine information from the individual and the population level. In a second step (see chapter 4), the individual level model will be substituted by a mechanistical approach by using an energy allocation model. Growth and reproduction of an individual are modelled by physiological rates that altogether represent a closed carbon budget. In addition, a physiologically structured population model is used for an efficient simulation on the population level. Finally, in chapter 5 the model framework will be used to study the underlying physiological adaptations of life-history shifts of *Daphnia* and its adaptive value under positive size-selective predation by visually feeding fish. In order to account for individual variability, experimental data of 9 coexisting clones of *Daphnia*, that had been reared with and without fish kairomones, have been used for this analysis. This model application shows the close links between physiology and

individual life-history and its adaptive value in an evolutionary context. An inclusion of the model system of *Daphnia* presented here within models on the ecosystem scale (e.g. water quality management models) is recommended and would potentially be of advantage for both, applied and fundamental research in limnology. In a conclusive chapter the advantages of a species-oriented modelling approach to *Daphnia* and possible further applications are discussed (chapter 6).

2 Basic aspects, recent developments, and current problems in zooplankton modelling

Within the classical food web of the pelagic zone, herbivorous zooplankton is situated between primary producers (i.e. algae and cyanobacteria) and higher trophic levels like planktivorous fish or invertebrate predators (Fig. 2.1). This food web is energetically maintained by the production of particulate organic carbon (POC) through photosynthesis (primary production). Alternative food sources to zooplankters are detritus or components of the microbial food web consisting of bacteria and protozoans (JÜRGENS *et al.*, 1994, 1996; HERBST, 1998). Dissolved organic carbon, e.g. delivered by sloppy feeding or exsudation, constitutes the nutritional basis of the microbial food web, which can include several trophic levels with complex direct and indirect interactions (e.g. WEISSE, 1991; ARNDT, 1993; ARNDT *et al.*, 1993; NIXDORF & ARNDT, 1993). Interactions between the classical food web and the microbial food web can be considerable and important in terms of their quantitative contribution to zooplankton growth — particularly when *Daphnia* dominates the zooplankton community (JÜRGENS *et al.*, 1994; JÜRGENS *et al.*, 1997; KAMJUNKE & ZEHRER, 1999; KAMJUNKE *et al.*, 1999). However, the major concern of modelling efforts to freshwater planktonic communities is still focused on the classical food web since components of the microbial food web are seldom tracked in standard monitoring programmes and acting processes are complex and not completely understood.

Herbivorous zooplankton, and *Daphnia* in particular, can exert strong grazing pressure on the phytoplankton and potentially lead to increased water transparency (e.g. LAMPERT *et al.*, 1986). The efficiency of this trophic interaction between phyto- and zooplankton depends strongly on phytoplankton community structure since *Daphnia* grazing is impaired by large colonies or filamentous algae. Their ability to control

algal blooms has attracted the attention of applied limnologists to daphnids. Indeed, *Daphnia* plays a central role in biomanipulation owing to direct grazing effects on the one hand and indirect effects on nutrient recycling on the other hand (SHAPIRO & WRIGHT, 1984; BENNDORF, 1987, 1990, 1995; BENNDORF *et al.*, 2002). Many studies have shown the ability of zooplankters, particularly of *Daphnia*, to act as a sink for phosphorus (VANNI & LAYNE, 1997; VANNI *et al.*, 1997; SOMMER *et al.*, 2003). Another topic of interest is the relevance of zooplankton for fish production by linking assimilated biomass of primary producers to higher trophic levels (HANSON & LEGGET, 1982; HÅKANSON & BOULION, 2001), which as well interacts with the recycling of nutrients (VANNI & LAYNE, 1997; VANNI *et al.*, 1997). Therefore, a comprehensive view on lake ecosystems as promoted by scientists as well as modern water quality managers cannot be achieved without taking the trophic interactions of zooplankters in general, and of *Daphnia* in particular, into account.

2.1 The significance of *Daphnia* in water quality management models

Considering the major role of the genus *Daphnia* in the functioning of lake ecosystems and their management by man, it is surprising to note that models on the ecosystem scale do seldom, if ever, account for zooplankton in the necessary complexity; their significance in the real system is hardly mirrored by their significance in model systems. Such lake models, further on called 'water quality management models' (WQM-models), are appropriate tools in research on ecosystem dynamics and in applied water quality management. For the latter, WQM-models are used to test the effects of changes in the environment (e.g. water level fluctuations, heat pollution) or to evaluate alternative restoration measures by scenario analysis (BENNDORF & RECKNAGEL, 1982; JAYAWEERA & ASAEDA, 1996; LEWIS *et al.*, 2002; ELLIOTT & THACKERAY, 2004; PUIJENBROEK *et al.*, 2004; ROMERO *et al.*, 2004). In fact, there are still a number of WQM-models in application (and development) that even lack a zooplankton compartment (Table 2.1). Those approaches use an implicit representation of zooplankton, i.e. zooplankton grazing is modelled as a dynamic grazing rate on phytoplankton without including a state variable 'zooplankton'. Those models payed a great deal of attention to the physical representation of the water body (Table 2.1).

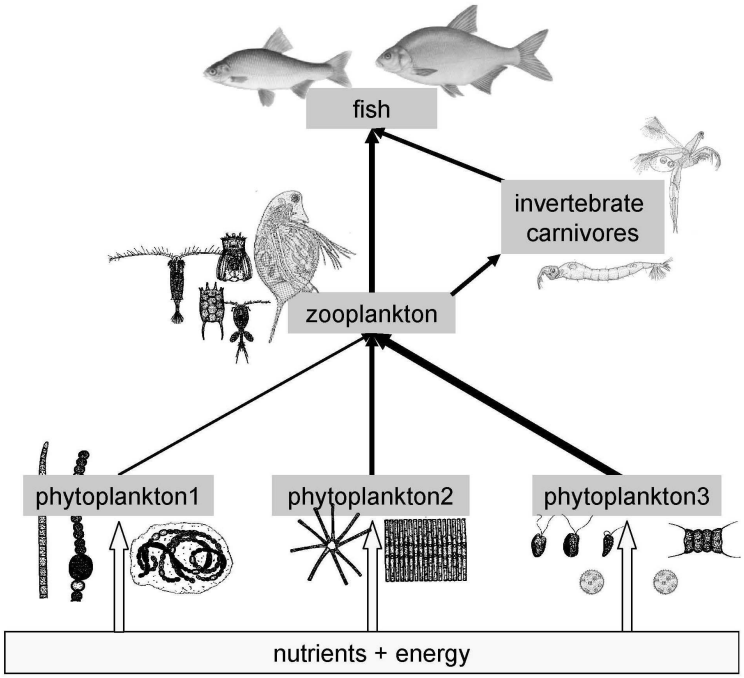

Figure 2.1: The classical food web in the pelagic zone of lakes and reservoirs. Grazing of herbivorous zooplankton (rotifers, copepods, cladocerans) on primary producers depends on the phytoplankton community structure because filaments (phytoplankton1), large colonies (phytoplankton2) or other defence strategies of some algal functional types partly protect those algae and cyanobacteria from being ingested by zooplankters (indicated by thin lines). Main predators of herbivorous zooplankton are invertebrate predators (*Chaoborus, Leptodora*) and planktivorous fish.

The remaining two model approaches in Table 2.1, which include a full state variable zooplankton (explicit representation), apply a standard population level approach with a single, lumped zooplankton group. Both models are hard to compare since SALMO (BENNDORF & RECKNAGEL, 1982) was developed almost 20 years earlier than the Biogeochemical Model of Lake Zürich (OMLIN *et al.*, 2001). Furthermore, SALMO has been successfully applied to many lakes and reservoirs with varying morphology and trophic state whereas the model of OMLIN *et al.* was applied only to Lake Zürich so far. And most important, the parameterization of SALMO is based on literature values and laboratory experiments while parameter fitting was applied to the Biogeochemical Model of Lake Zürich. For that reason, both models are almost diametrical in terms of their modelling philosophy. For reviewing model structure and outputs of the zooplankton compartment it, therefore, appears more conclusive to

Table 2.1: Comparison of selected water quality management models with respect to the main focus of their biological part, the representation of hydrophysics, and the representation of zooplankton.

Model	Focus of the biological part	Hydrophysics	Zooplankton
CE-QUAL-W2 (WELLS, 1997)	water quality management, eutrophication, two-dimensional realization	complex approach	implicit representation (no state variable)
WASP (V7.0) (DI TORO *et al.*, 1983)	contaminant fate and distribution, eutrophication, 1D to 3D realization possible	complex approach	implicit representation (no state variable)
PROTECH (REYNOLDS *et al.*, 2001)	phytoplankton succession, competition for resources	simple approach	implicit representation (no state variable)
DYRESM-WQ (HAMILTON & SCHLADOW, 1997)	interaction of hydrophysical and biological processes	complex approach	implicit representation (no state variable)
Biogeochemical Model of Lake Zürich (OMLIN *et al.*, 2001)	nutrient cycling, detritus dynamics, sedimentation, sediment-related processes	complex approach	explicit representation as state variable (only one group)
SALMO (BENNDORF & RECKNAGEL, 1982)	eutrophication, direct and indirect trophic interactions, water quality management	no	explicit representation as state variable (only one group)

focus on SALMO.

Interestingly, most parameter values in the zooplankton compartment of SALMO were derived from empirical studies using *Daphnia* as model organism. However, simulation outputs for zooplankton are usually going to be compared with observations of total zooplankton. Consequently, this state variable is considered to represent the whole guild of herbivorous zooplankton (e.g. rotifers, copepods, cladocerans), i.e. no functional differentiation between taxa is implemented. Although empirical limnologists have accumulated broad evidence that zooplankton taxa significantly differ in their trophic interactions within the food web and would hardly follow to put all those taxa in one functional group (FULTON, 1988; SOMMER *et al.*, 2001; KAGAMI *et al.*, 2002), simulation outputs of SALMO are quite acceptable. Estimation of standing crops by SALMO is generally viewed as being surprisingly well predicted and

in water bodies of lower trophic state timing and principal dynamic development can be met. Nevertheless, zooplankton dynamics in meso- to eutrophic waters still face a problem, particularly the simulation of long-lasting clear water phases or summer depressions of zooplankton. Recent investigations have indicated that the processes involved herein are complex and not solvable by increasing the functional or taxonomical resolution of the zooplankton submodel, which will be outlined below. Consequently, simulation outputs for zooplankton are in many cases not satisfying and, in fact, several authors have stated zooplankton to be difficult to model (HAMILTON & SCHLADOW, 1997; OMLIN *et al.*, 2001).

2.2 Resource overexploitation and the spring clear water phase

Evaluation of WQM-model outputs, i.e. the comparison of model outputs with respective measurements of the real world, is subjective and many modellers recommend to rather focus on characteristic patterns than on the reproduction of measurements in an exact quantitative manner (pattern-orientated modelling, GRIMM *et al.*, 1996). Concerning the role of zooplankton in plankton succession two characteristic patterns emerge that are of ample importance for WQM-models:

1. a pronounced clear water phase initiated by mass development of zooplankters (mostly *Daphnia*) in spring or early summer (LAMPERT *et al.*, 1986), sometimes followed by a midsummer decline of *Daphnia*, and

2. a shift in phytoplankton composition towards poorly ingestible algae during summer (SOMMER *et al.*, 1986) induced by zooplankton grazing.

Both patterns, which are of particular interest for water quality management purposes, are direct responses to zooplankton grazing. Existing WQM-models are well capable of reproducing the shift in phytoplankton composition towards poorly ingestible algae (e.g. REYNOLDS *et al.*, 2001; PETZOLDT & SIEMENS, 2002). However, a phenomenological reproduction of the spring clear water phase was proven to be problematic in many model simulations, particularly when applied to eutrophic water bodies (OMLIN *et al.*, 2001; RINKE *et al.*, 2004).

Empirical studies on population dynamics of *Daphnia* during spring and early summer revealed high fluctuations in population demography (HÜLSMANN, 2003;

WINDER *et al.*, 2003; WAGNER *et al.*, 2004). At the end of the spring algal bloom a very strong cohort of daphnids is born that will have consumed all resources available before becoming mature. This peak cohort is born into an environment becoming scarce of resources, which implies high physiological stress on these individuals resulting in an elevated non-consumptive mortality sooner or later (HÜLSMANN, 2003). Subsequently, these processes lead to a declining population size of *Daphnia*, which in some cases, particularly in eutrophic waters, can directly proceed to the initiation of a midsummer decline[1] of *Daphnia* (HÜLSMANN & WEILER, 2000; HÜLSMANN, 2003; WAGNER *et al.*, 2004). Researcher originally believed predation by young-of-the-year (YOY) fish to be the ultimate cause of a midsummer decline but empirical studies have not supported this hypothesis (MEHNER *et al.*, 1998a). Only recently, it was proven that only the coaction of fish predation and non-consumptive mortality, induced by senescence and starvation, is sufficient to induce a midsummer decline (BENNDORF *et al.*, 2001; WAGNER *et al.*, 2004). Consequently, the timing of predation pressure and non-consumptive mortality, which is controlled by temperature in early spring, is essential for this phenomenon. In conclusion, apart from low food conditions and fish predation the development of population demography was proven to be responsible for this population collapse. Due to physiological stress during the clear water phase, individuals of the peak-cohort display a high age at maturity, which roughly equals life expectancy, i.e. many individuals die before they reproduce (HÜLSMANN, 2003). Sometimes, if the peak cohort of the population is neatly synchronized, this can result in a sudden breakdown of *Daphnia* abundance (HÜLSMANN & WEILER, 2000). Altogether, the vast overexploitation of their algal resources by *Daphnia* marks the begin of a cascade of events resulting in a pronounced, long-lasting clear water phase, which might be followed by an almost complete collapse of the *Daphnia* population. In conclusion, the processes involved in this resource overexploitation are key mechanisms in zooplankton population dynamics and should be included in the respective ecological models.

In this respect it is worth analyzing the mechanisms that concur to the massive overexploitation of resources by *Daphnia* during the clear water phase. Besides high specific grazing rates of *Daphnia*, which lead to rapidly diminishing resources, also demographic effects are responsible for this phenomenon. In particular, delaying effects induced by the life-cycle of cladocerans intensify the resource overexploitation.

[1] the breakdown in daphnid abundance during summer.

Three different processes are involved in these delaying effects: Firstly, there is a delay in daphnid reproduction because cladocerans deposit their eggs into a brood chamber where eggs remain for one molting cycle and embryogenesis takes place. Approximately 2.5 (at 20°C) to 4.5 (at 15°C) days are needed for this embryogenesis (BOTTRELL *et al.*, 1976). Thus, current reproduction in terms of newborns released into the population corresponds to the egg production (i.e. to the nutritional status) of the population about 3-5 days ago. Generally speaking, at the beginning of the clear water phase when food concentration in the environment is becoming critically low reproduction still proceeds for a couple of days.

Secondly, when resources have been diminished, feedback mechanisms of food shortage on the population rate of change are delayed. Individuals can survive a distinct period of starvation without suffering additional mortality (LEMCKE & LAMPERT, 1975; ELENDT, 1989). Starvation resistance also depends on the physiological state of the individual, which might interact with individual age (TESSIER *et al.*, 1983; ROMANOVSKY, 1985). *Daphnia* can even partly prepare itself for starvation by reducing fecundity and increasing reserve content of eggs (CLEUVERS *et al.*, 1997). This switch, which might be viewed as a shift from r-strategy to K-strategy, was proven to be inducible by crowding (CLEUVERS *et al.*, 1997). Thus, as soon as the clear water phase has been initiated the *Daphnia* population is starving but, however, starvation related mortality occurs only a couple of days later.

Thirdly, cladocerans need to grow up to a specific size (size at maturity) before becoming mature. In *Daphnia*, this juvenile development takes at least 4 days if environmental conditions are optimal but can be considerably prolonged if temperature or food conditions are poor. Hence, there is a delay between the release of offspring and its contribution to population growth. This makes population growth rate strongly dependent on population demography. A strong cohort of individuals that is becoming mature will cause a dramatic increase in population growth rate — even if environmental conditions are rather constant. This reveals an interplay between the history of the population, as memorized in its demography, and the current dynamics of the population, which consequently are not solely dependent on current environmental conditions.

2.3 Empirical evidence from field observations

Own investigations[2] of *Daphnia* population dynamics in the eutrophic Bautzen reservoir (surface area: 533 ha, mean depth: 7.4 m, for details see KÖNIG *et al.*, 2005) also provide strong support for the complex interactions of population demography and the initiation of the clear water phase and a subsequent midsummer decline (Figs. 2.2 and 2.3). At the beginning (08. May) of population development the *Daphnia* population showed a negative exponential size distribution as typical for exponentially growing populations. In this period the peak cohort was formed, which soon after its establishment ceased growth due to food limitation during the clear water phase (16. May). At that time, individuals of the peak cohort were still immature. Afterwards, increased mortality, possibly induced by starvation, led to a decline of the population until the end of May. Due to a mass development of *Fragilaria crotonensis* in June consisting of large colonies that were not ingestible by *Daphnia*, recruitment of the population was low. Consequently, ageing of the population proceeded further and, finally, a large part of the population died before becoming adult because of senescence. Additionally, at the end of June predation by fish increases as indicated by the vanishing of larger size classes due to positive size-selective predation (compare LAZZARO, 1987). Former studies in the Bautzen reservoir revealed predation by YOY perch on *Daphnia* to be most pronounced during June (WAGNER *et al.*, 2004). However, daphnids can cope at least partially with fish predation by life-history adaptations in terms of reduced size at maturity (MACHÁČEK, 1991; SPAAK *et al.*, 2000) as can be seen in the samples of July. Afterwards, further population growth was prevented until the end of August possibly due to the dominance of poorly ingestible algae. At that time, a mass development of *Microcystis aeruginosa* occurred in Bautzen Reservoir. Although some studies showed that this cyanobacteria can be ingestible and support significant daphnid populations (DE BERNARDI *et al.*, 1981; BENNDORF *et al.*, 1988) most investigations haven proven them to be poorly ingestible, toxic, and of poor nutritional quality (LAMPERT, 1982; JUNGMANN *et al.*, 1991; DEMOTT, 1999; LÜRLING, 2003).

[2] biweekly sampling with tube samplers at 5 depths (0, 3, 5, 8, and 10 m)

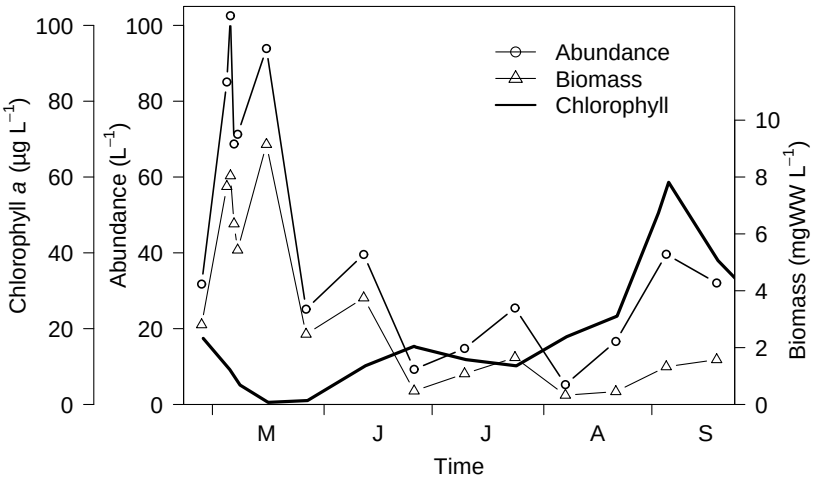

Figure 2.2: *Daphnia* abundance and biomass in the Bautzen Reservoir in 2003. Values were calculated as weighted means of sampling depths. Chlorophyll *a* was measured by a fluorescence probe (bbe Moldaenke, Germany).

2.4 Implications for water quality management models

To summarize, the facts mentioned so far indicate that the mechanisms involved in population dynamics of zooplankton are complex and existing approaches to the simulation of zooplankton in lake models are far away from accounting for this complexity. Even more, the classical population level approach is not applicable to this problem because population dynamics are more than a simple difference between source and sink terms. In addition to resource limitation and density dependence other factors come into play (e.g. population demography or individual life-history). All these processes are already well documented by empirical scientists but rarely recognized by those working on the development of WQM-models. In particular, three properties of zooplankton populations appear to be of major concern:

1. life-cycle and individual life-history (e.g. relevant for juvenile development, embryogenesis, life-history adaptations)

2. physiological properties of the individuals within the population (e.g. relevant for starvation resistance, senescence, size-scaling of physiological rates)

3. information about population demography (e.g. relevant for demographic effects in population growth, size-selective mortality, memory effects)

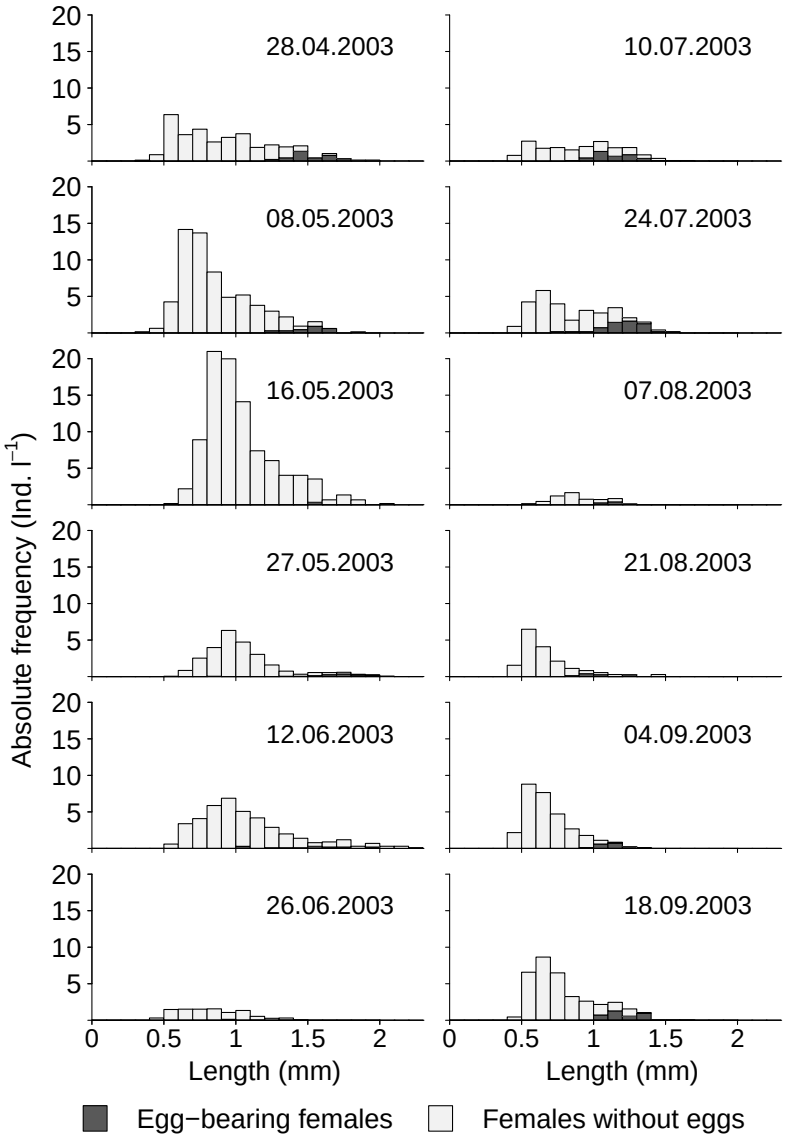

Figure 2.3: Demography of the *Daphnia galeata* population in Bautzen Reservoir in 2003. Size-structure of the population is given for each sampling date (indicated in the upper right corner of each graph). Egg-bearing individuals within each size-class are drawn as dark columns.

To succeed on this line of arguing it explicitly emerges that a completely new model structure is necessary for such a purpose. Instead of promoting a functional diversification of the guild of herbivorous zooplankton in WQM-models, as have been implemented by other authors (e.g. SCAVIA, 1980; HÅKANSON & BOULION, 2002), emphasis should be given to alternative modelling concepts, that take both information from the individual and population level into account.

In this respect it is worthwhile to review existing model frameworks in theoretical ecology that provide a number of possible approaches to this problem. More than 15 years ago, theoretical ecologists recognized the large influence of individual level processes on population dynamics and started to develop individual based models (KAISER, 1979; DEANGELIS & ROSE, 1992; MOOIJ & BOERSMA, 1996; RATTE, 1996; MOOIJ *et al.*, 1997). Although the contribution of individual based models (IBM) to general ecological theory was less than expected (GRIMM, 1999) they have provided a new framework to account for the complexity of ecological systems and opened a new perspective in population ecology. However, one of the basic properties of IBMs is their high computational demand, which limits its application to scientific purposes. Large ecosystem models used in applied ecology, e.g. WQM-models, have to guarantee an efficient simulation in order to provide results within a relatively short time. Thus, a higher level of aggregation is required to realize a reduced computation time. One solution to this is the aggregation of similar animals within cohorts or superindividuals (DE ROOS *et al.*, 1992; SCHEFFER *et al.*, 1995). In particular, the concept of physiologically structured population models by DE ROOS *et al.* (1992), which even has been applied to zooplankton populations, provides a useful approach because (i) individual and population level are organized in modules, (ii) all dynamic processes can be described by ordinary differential equations making it conveniently applicable in WQM-models, and (iii) a comprehensive mathematical theory including analytical solutions for specific purposes is available (DE ROOS, 1997).

Besides an efficient and more realistic simulation of population dynamics, the usage of physiologically structured population models (PSPM) would possibly act as a bridge between theoretical and applied ecology. Many applications to current issues of theoretical ecology have shown the usefulness of PSPM or related concepts, e.g. on population dynamics, competition, metabolic organization, spatial ecology, and stoichiometric theory (e.g. NISBET *et al.*, 1989; DE ROOS *et al.*, 1992; GURNEY *et al.*, 1996; NOONBURG *et al.*, 1998; DE ROOS *et al.*, 2002; ANDERSON *et al.*, 2005; HÜLSMANN *et al.*, 2005). Unfortunately, theoretical studies are in most cases restricted to a clearly defined complex of problems and do seldom actively propagate the implications of their results to ecosystem functioning or applied issues. More unfortunately, applied ecologists and scientists working on the ecosystem level do apply models that mostly lack the appropriate structure to integrate recent results from theoretical and fundamental ecology. It therefore appears to be important to make

knowledge from theoretical and fundamental research more easily accessible for scientists working on higher levels of biological organization (e.g. on the ecosystem scale). A framework for this idea could be provided by a species-oriented model approach. In general, ecology would take profit if model frameworks would span over several levels of biological organization, i.e. from cells and tissues over individuals and populations to the ecosystem (KOOIJMAN, 2000). As a first step in this direction, standard population level approaches may be substituted by physiologically structured population models. In terms of zooplankton in lake models, such an inclusion of an PSPM-approach would allow the simulation of several processes proven to be relevant in the field but classical population level models cannot cope with, e.g. size selective predation, life history adaptations, non-consumptive mortality, and physiological stressors.

3 An empirical approach to individual life-history and population dynamics of *Daphnia* by using multiple regression models[1]

Abstract

Individual based simulations of population dynamics require the availability of growth models with adequate complexity. For this purpose a simple-to-use model (non-linear multiple regression approach) is presented describing somatic growth and reproduction of *Daphnia* as a function of time, temperature and food quantity. The model showed good agreement with published observations of somatic growth (r^2 = 0.954, n = 88) and egg production (r^2 = 0.898, n = 35). Temperature is the main determinant of initial somatic growth and food concentration is the main determinant of maximal body length and clutch size. An individual based simulation was used to demonstrate the simultaneous effects of food and temperature on the population level. Evidently, both temperature and food supply affected the population growth rate but at food concentrations above approximately 0.4 mg C L^{-1} *Scenedesmus acutus* temperature appeared as the main determinant of population growth. Four simulation examples are given to show the wide applicability of the model: (1) correlation between population birth rate and somatic growth rate, (2) contribution of egg development time and delayed somatic growth to temperature-effects on population growth, (3) comparison of population birth rate in simulations with constant vs. food-dependent size at first reproduction and (4) costs of diel vertical migration. Due to its plausible behavior over a broad range of temperature (2 - 20°C) and food conditions

[1] Main results of this chapter have been published in RINKE, K. & T. PETZOLDT, 2003: Modelling the effects of temperature and food on individual growth and reproduction of *Daphnia* and their consequences on the population level: an empirical approach. Limnologica 33, 293-304.

(0.1 - 4 mg C L^{-1}) the model can be used as a module for more detailed simulations of *Daphnia* population dynamics under realistic environmental conditions.

3.1 Introduction

Studies about population dynamics of *Daphnia* have shown the necessity to investigate individual level processes, which can contribute substantially to our understanding of the population level. Well studied examples of such relevant individual level processes are, for example, size selective predation or increased mortality through senescence (e.g. LYNCH, 1979; GURNEY *et al.*, 1990; MOOIJ *et al.*, 1997; HÜLSMANN & WEILER, 2000; HÜLSMANN, 2003). Therefore, modelling approaches to these phenomena have to be focused on the individual level and the development of such models implies a strong demand for a detailed description of individual ontogeny and reproductive potential. Numerous investigations have dealt with the description of daphnid growth and reproduction in relation to environmental conditions (e.g. RICHMAN, 1958; HALL, 1964; VIJVERBERG, 1976; LAMPERT, 1978; GLIWICZ & LAMPERT, 1990; GIEBELHAUSEN & LAMPERT, 2001) and both processes are, of course, influenced by a number of environmental factors whose comprehensive description is still a challenge for ecologists. Among existing model approaches the concept of dynamic energy budget models (DEB-models, see KOOIJMAN, 2001, formerly known as energy allocation models) appeared to be the most convincing approach simply because of its mechanistic methodology (e.g. PALOHEIMO *et al.*, 1982; KOOIJMAN & METZ, 1984; GURNEY *et al.*, 1990; HALLAM *et al.*, 1990). Growth and reproduction of individuals are modelled on basis of a carbon budget and detailed physiological information about ingestion, assimilation and metabolism is integrated. Nevertheless, available DEB-models of *Daphnia* still display limitations in their applicability to the simulation of *Daphnia*-populations under field conditions because of two reasons: (i) they either were purely focused on food dependent dynamics and assumed a constant temperature (mostly 20°C, e.g. GURNEY *et al.*, 1990; HALLAM *et al.*, 1990) or (ii) comprehensive validation of model outputs on independent data have not been carried out (e.g. WULFF, 1980; KOH *et al.*, 1997). Of course, introduction of variable temperature into such models demands very detailed knowledge about temperature reaction norms of all physiological rates of *Daphnia*, which may be still problematic.

Recently, MOOIJ *et al.* (2003) modelled somatic growth and egg production of

Daphnia galeata in the field using a multiple regression approach without the explicit description of physiological processes like ingestion, assimilation or metabolism. With this empirical approach they successfully simulated the dynamics of a field population under variable conditions of food and temperature. However, their approach utilized food supply only indirectly by an observed standard egg production, which is needed as external forcing data by the model. Therefore, this model cannot be applied to such situations where egg production data are not available. For independent applications that are related to field conditions it would rather be preferable to have egg production as an explicit output of the model; this would allow the application of food supply and temperature as independent variables and the calculation of somatic growth and egg production as dependent variables. The advantage of such an empirical approach would be a less exhaustive demand for data describing the dynamics of all relevant processes (which in most cases are not easily available) and the simplicity of its model structure allowing a straightforward applicability. Furthermore, an empirical approach might release computational resources that can be used for other intended study aims (e.g. spatially explicit simulations, community dynamics). In conclusion, many model studies of *Daphnia*, in particular those focusing on field conditions, do not necessarily require a completely mechanistic approach.

The morphology and thus the ontogenetic development with its accompanying patterns in reproduction differ quantitatively between species within the genus *Daphnia*. Therefore, a model of *Daphnia* has to be focused on a distinct group of similar species to minimize the influence of interspecific differences. In this study the *Daphnia galeata/hyalina* species complex comprising *D. galeata*, *D. hyalina*, *D. cucculata* and their hybrids (FLÖSSNER & KRAUS, 1986; SCHWENK & SPAAK, 1995; SPAAK & BOERSMA, 2001) have been chosen, which are typical and widespread inhabitants of the pelagic zone of temperate lakes. In particular, the two species *D. galeata* and *D. hyalina* are closely related to each other and show similar morphological properties (WOLF & MORT, 1986; FLÖSSNER, 2000). Consequently, the model was exclusively developed on growth data of either one of these species or their hybrid *D. galeata* $\times$ *hyalina*. Although the current parameterization is restricted to this species complex, the presented model framework allows the simulation of other species of the genus *Daphnia* supposing adequate individual level data are available for parameterization.

The aim of this study was to develop a tool for the estimation of somatic growth and reproduction of *Daphnia*, based on an empirically derived simple-to-use model

formulation that was calibrated on experimental data of *D. hyalina/galeata*. As a new outcome, the model allows the quantitative study of the effects of both food and temperature on individual growth and reproduction as well as on population growth. For the latter, the model formulation will be applied within an individual based simulation. Finally, four exemplary applications of the model will show its general applicability. The quantitative view presented should provide a contribution to the understanding of the dynamic development of individual daphnids and natural *Daphnia*-populations.

3.2 Methods

3.2.1 Model of growth and reproduction

A non-linear multiple regression approach was chosen for the model formulation, which basically consists of the two components somatic growth and reproduction. Food supply and temperature of the environment have to be provided as input variables and further environmental factors (e.g. food quality) have been intentionally neglected. Literature data from experimental studies were used for the construction and calibration of the model. The increase of body length was modelled as a continuous process although in reality somatic growth (in terms of length increase) of *Daphnia* almost only occurs after molting and thus stepwise. However, this facilitated the application of common parameter estimation procedures for the calibration of the model, because model outputs for growth and reproduction are a continuous function of time.

Only parthenogenetic reproduction was considered, which might be split into the two subprocesses egg production (clutch size) and the development of eggs into embryos (egg development time). Whereas egg development of *Daphnia* can be thoroughly described as a process solely dependent on temperature (BOTTRELL *et al.*, 1976; KERFOOT, 1985; SAUNDERS *et al.*, 1999), egg production is not yet characterized satisfactorily. Therefore, our approach of describing daphnid reproduction is focused on describing the dependence of egg production on temperature and food. In the individual based simulation, egg development time was calculated according to BOTTRELL *et al.* (1976).

The model was constructed stepwise. Firstly, appropriate functional relationships between independent (temperature, food concentration) and dependent variables (so-

matic growth, egg production) were tested and progressively defined. The goodness of fit was examined graphically and by using the coefficient of determination (r^2). A baseline model containing employable functional relationships - but an inadequate parameterization - was the result of this first step. In a second step, the parameterization of the baseline model was calibrated on a broad basis of experimental data in order to achieve a generalized model formulation that displayed quantitatively realistic model behavior. The statistical computations (explorative ANOVA/ANCOVA and parameter estimation of the non-linear multiple regression via a Gauss Newton algorithm) were conducted with the statistical package **R** (IHAKA & GENTLEMAN, 1996, R Development Core Team: see www.r-project.org).

3.2.2 Individual based simulation

In order to assign the individual level effects of food and temperature to the population level, an individual based simulation (DEANGELIS & ROSE, 1992) was carried out. The simulations (time step 1h) were performed using the JAVA language (Sun Microsystems). All runs of the individual based model (IBM) started with one neonate *Daphnia* and simulated the population development over 60 days. Size of neonates was set to 0.65 mm corresponding to observations in the publications used for model calibration. Size at first reproduction was set to 1.5 mm (STICH & LAMPERT, 1984; SPAAK *et al.*, 2000; HÜLSMANN, 2001). Individual life history in the IBM was implemented in accordance with *Daphnia* life-cycle. Individuals deposit the first clutch of eggs in their brood pouch at the time they reach size at first reproduction (SFR). Hatchlings from these eggs were released as neonates (i.e. age t=0) at the next molt of the mother. In *Daphnia*, the time between two molts is about equal to egg development time (BOTTRELL *et al.*, 1976; VIJVERBERG, 1980). Individual clutch sizes at that time a new clutch is laid were calculated according to the model specification (see below). No mortality and no density dependent processes were applied to the population leading to an exponential growth. The sum of all individuals born in a simulation indicates the growth potential of the population at the respective food and temperature conditions. Therefore, population birth rate b was used (Eq. 3.1) to assess individual fitness and is interpreted as an integrated measure of both individual somatic growth (larger animals produce larger clutches) and reproduction.

$$b = \frac{\ln(X_{t1}) - \ln(X_{t0})}{t_1 - t_0} \tag{3.1}$$

Note, that the starting population in this simulation study displayed no stable age distribution, but comprised only of one single neonate individual (age t=0), i.e. mimicking the conditions in the pelagic zone of temperate lakes in spring when *Daphnia* starts to build up its population out of a few individuals[2]. A systematic set of combinations of food (in the range of 0.1 - 4 mg C L^{-1} *Scenedesmus acutus*) and temperature (in the range of 2 - 20°C) was applied to the simulation.

3.2.3 Model applications

In order to demonstrate possible fields of application and to critically evaluate quantitative outcomes of the model approach four model applications were specified, each focused on rather different fields of current research on *Daphnia*.

1. **Correlation between juvenile somatic growth and population birth rate:** In experimental studies, the juvenile somatic growth rate was found to be strongly correlated with population birth rate (LAMPERT & TRUBETSKOVA, 1996); therefore, model outputs for population birth rate were compared with those of individual somatic growth rate. The model specification for somatic growth was used to calculate a juvenile growth rate g according to LAMPERT & TRUBETSKOVA (1996) by using the increment in body mass from the age of 0 to 4 days.

$$g = \frac{\ln(W_{a=0}) - \ln(W_{a=4})}{t_{a=4} - t_{a=0}} \tag{3.2}$$

   The individual body weight was calculated using the body length-weight relationship of *D. hyalina* taken from GELLER (1989).

2. **Effects of temperature on population birth rate:** At decreasing temperatures, longer egg development times as well as delayed somatic growth should both lead to smaller population birth rates. But in reality it is not possible to separate these two effects from each other. However, by using the model this can be

[2]The starting population is either comprised of surviving winter individuals or of hatchlings from resting eggs (ephippia).

done by modifying the model specification in such a way that somatic growth took place according to ambient temperature but egg development time was set to the corresponding value at 20°C. This modified model specification was applied at different temperatures and model outputs (i.e. population birth rate *b*) were compared with those from the respective standard scenarios. This procedure excluded the influence of egg development time from the temperature effects on population growth rate, which opens the possibility to quantify how delayed maturity – the solely remaining factor – affects the population growth rate. This comparison was carried out at a limiting and a non-limiting food concentration (0.1 and 0.75 mg C L^{-1}). An important issue of this model application is the fact that in population models of *Daphnia* that are often applied within lake models the well documented temperature-dependence of egg development time is used in order to calculate temperature effects on population birth rate (e.g. BENNDORF, 1979). This is done for the sake of simplicity and because of difficulties in accounting for delayed maturity due to lowered somatic growth in such models, which are purely focused on the population level and cannot account for individual level processes.

3. **Food-dependent size at first reproduction (SFR):** Experiments by BOERSMA & VIJVERBERG (1995b) demonstrated that SFR decreased with declining food concentration (data at 17.5 °C and 0.13, 0.25, 0.5 and 2.5 mg C L^{-1}). The effect of this variable SFR on population growth was quantified by comparing a scenario using the variable SFR as found in BOERSMA & VIJVERBERG (1995b) with a standard scenario using a fixed SFR.

4. **Costs of diel vertical migration:** The observations of STICH (1989) provided a detailed description of the diel vertical migration (DVM) of *Daphnia hyalina* in Lake Constance. Individuals were found in hypolimnetic waters during day and in epilimnetic waters during the night. The migration behavior is mainly triggered by fish infochemicals and secondary phototaxis (RINGELBERG, 1999; VON ELERT & POHNERT, 2000) but predation by visually feeding fish was found to be the ultimate factor of DVM, which is the subject of the predator avoidance hypothesis (ZARET & SUFFERN, 1976; LAMPERT, 1993a). Costs of DVM are associated with lower temperature and food concentration in deeper water layers (DAWIDOWICZ, 1994). In his study, STICH (1989) provided tem-

peratures and food concentrations at the mean population depths during day and night of the population (data from 15th/16th August 1977 were used). Food concentrations were measured as mg carbon per litre of $POC < 30\,\mu$m. According to MÜLLER-NAVARRA & LAMPERT (1996) this food concentration was divided by 2 to take roughly into consideration food quality and estimate food in terms of mg C per litre of *Scenedesmus acutus*. Birth rates of the migrating population were calculated as time-weighted mean of birth rates during day and night and compared with animals that would have spent the whole day in epilimnetic waters .

3.3 Development of the model

3.3.1 Baseline model

We examined the data of HALL (1964) in order to find a satisfying set of functions describing the kinetics of growth and reproduction under varying conditions of temperature and food. HALL (1964) simultaneously investigated somatic growth and egg production of *Daphnia galeata mendotae* in relation to three different temperatures (11°C, 20°C and 25°C) and three food levels. The food supply consisted of a mixture of *Chlorella* and *Ankistrodesmus* whereby *Ankistrodesmus* accounted for ca. 95% of individual abundance (D.J. HALL, *pers. com.*). Food concentration was expressed as Klett units (optical density measured with a Klett-Summerson photometer) and three different food levels were investigated (0.25, 1 and 16 Klett units). The value of 16 Klett units refers to approximately 106 cells ml^{-1}. The data from HALL (1964) offered the possibility to concurrently investigate effects of temperature and food supply on growth and reproduction on one consistent data set, which avoided deviations arising from different experimentalists or experimental setups.

3.3.1.1 Somatic growth

The model of somatic growth was based on the von Bertalanffy equation (VON BERTALANFFY, 1957) that is commonly used in models of daphnid somatic growth (e.g. KOOIJMAN, 1986; MOOIJ *et al.*, 1997):

$$L_t = L_{max} - (L_{max} - L_0) \cdot e^{-kt} \tag{3.3}$$

Here, L_t corresponds to the body length L (mm) of an individual at the age t (t=0 at hatching) and L_{max} and L_0 denote the maximal body length of adults and the body length of neonates, respectively. The von Bertalanffy growth coefficient k is responsible for the initial slope of the growth curve. For all combinations of food and temperature the parameter L_0 was set to 0.35 mm representing the mean value of the extrapolated growth curves at t=0 in Hall's data.

The parameter k showed an exponential increase (Eq. 3.4) with temperature (T). Food concentration appeared to have no significant effect on regression residuals (ANOVA, p = 0.42). In contrast to this, food concentration (F) was proven to strongly influence maximal body length (L_{max}) that was accounted for by using a Holling type II functional response term plus an additional constant. However, residuals of this model were still influenced by temperature (ANOVA, p = 0.049) and showed a negative trend towards higher temperatures. This trend became even more obvious when associating parameter k instead of temperature (Eq. 3.5). An overall parameter estimation procedure (non-linear least squares) successfully resulted in a parameterization (Table 3.1) that displayed a high coefficient of determination (Fig. 3.1, r^2 = 0.983, n = 110).

$$k = b_1 \cdot e^{b_2 T} \tag{3.4}$$

$$L_{max} = \frac{a_1 \cdot F}{a_2 + F} + a_3 - a_4 k \tag{3.5}$$

3.3.1.2 Egg production

Age-dependent individual clutch size at each factor combination of temperature and food concentration were derived from HALL (1964). Individual body length at the time of spawning was calculated using the somatic growth model described above. In accordance with HALL (1964) and further publications (e.g. STICH & LAMPERT, 1984; ARBACIAUSKAS & GASIUNAITE, 1996; HÜLSMANN, 2001) a linear increase of clutch size (E) with body length (L) was assumed (Eq. 3.6).

$$E = \alpha \cdot L + \beta \tag{3.6}$$

An ANCOVA of clutch sizes (body length as covariate revealed a significant effect of food concentration on the regressions of clutch size vs. body length, whereas nei-

Table 3.1: Parameter estimates for the multiple regression model of somatic growth (baseline model) fitted on the data set of HALL (1964) using eqs. 3.3, 3.4, and 3.5 (p = significance level).

Parameter	Value	Unit	Standard error	p
$a1$	1.167	mm	0.073	< 0.001
$a2$	0.573	$\mathrm{mg\,C\,L^{-1}}$	0.103	< 0.001
$a3$	1.42	mm	0.108	< 0.001
$a4$	2.397	d	0.623	< 0.001
$b1$	$5.11 \cdot 10^{-3}$	$\mathrm{d^{-1}}$	$4.6 \cdot 10^{-4}$	< 0.001
$b2$	0.122	$(^\circ\mathrm{C})^{-1}$	0.004	< 0.001
L_0	0.35	mm	fixed parameter*	—

*according to HALL (1964)

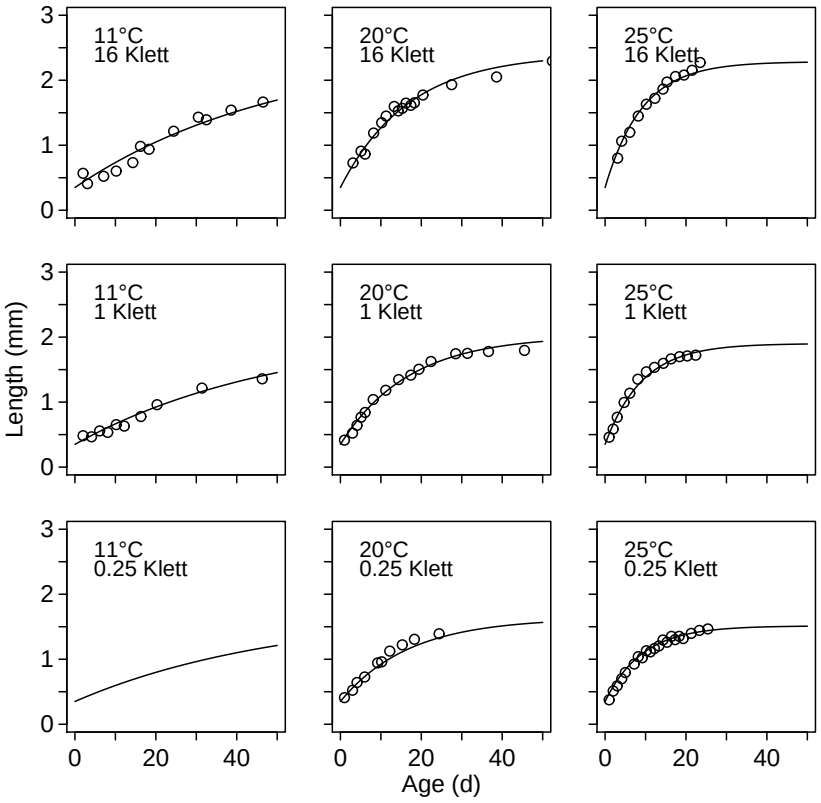

Figure 3.1: Comparison of the multiple regression model (lines) and the respective growth data (points, HALL, 1964) for different combinations of temperature and food concentrations. Food concentration is given as Klett units. No data were available for the combination 11°C and 0.25 Klett units (overall $r^2 = 0.983$).

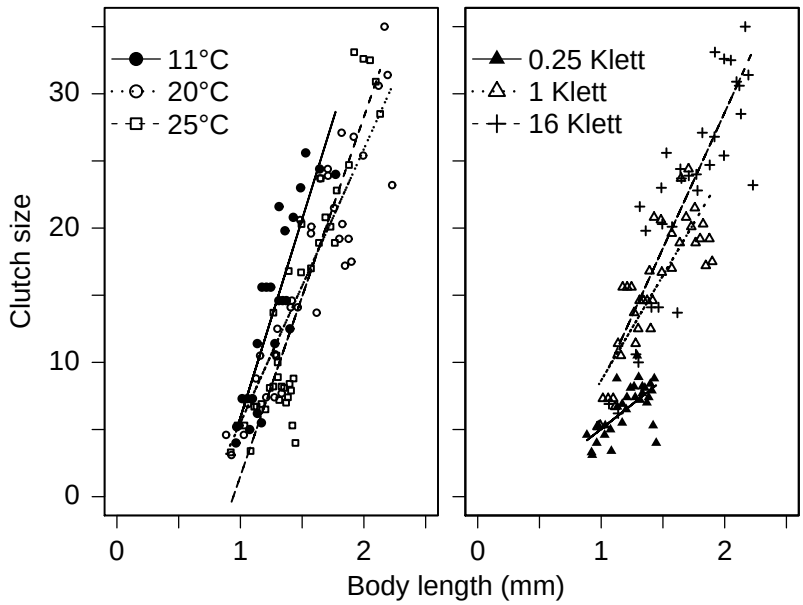

Figure 3.2: Linear regressions for clutch size against body length for different temperatures (left) and different food concentrations (right). Data were taken from HALL (1964). Slopes of all regressions were highly significant ($p < 0.001$ in all cases). Nevertheless, only food has a significant effect on the slopes and no significant effect of temperature could be found (Table 3.2)

ther an effect of temperature nor an interaction was found (Table 3.2 and Fig. 3.2). The slope α in Eq. 3.6 was calculated from food concentration by a Holling type II functional response model (Eq. 3.7). The intercept β in the linear regressions increased with rising food supply (Eq. 3.8). However, an examination of the significance of these parameters revealed a negligible influence of the parameter u_c although this parameter is needed for consistent dimensions. Therefore, a fixed value of 1 $(\mathrm{mg\,C\,L^{-1}})^{-1}$ was applied, i.e. u_c acts only as a unit conversion factor in order to provide dimensional correctness without providing another degree of freedom. Again, overall parameter estimation (non-linear least squares) was conducted and displayed a high coefficient of determination (Table 3.3, Fig. 3.3, r^2 = 0.872, n = 99).

$$\alpha = \frac{\alpha_{max} \cdot F}{K_\alpha + F} \tag{3.7}$$

$$\beta = \beta_{min} \cdot (1 - e^{-u_c F}) \tag{3.8}$$

Table 3.2: ANCOVA of individual clutch sizes with body length as covariate (data taken from HALL (1964), p = significance level).

Factor	df (effect)	df (error)	F	p
Food	2	89	17.58	< 0.001
Temperature	2	89	1.76	0.179
Interaction	4	89	2.13	0.084

Table 3.3: Parameter estimates for the calculation of clutch sizes using Eq. 3.7 and Eq. 3.8 (p = significance level).

Parameter	Value	Unit	Standard error	p
α_{max}	19.94	eggs	1.41	< 0.001
K_α	0.36	$\mathrm{mg\,C\,L^{-1}}$	0.03	< 0.001
β_{min}	-10.15	eggs	2.33	< 0.001
u_c	1	$(\mathrm{mg\,C\,L^{-1}})^{-1}$	—*	—*

*no free parameter

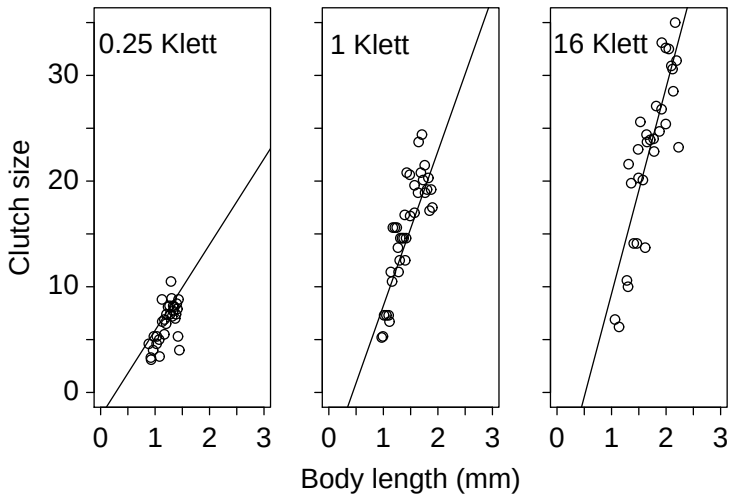

Figure 3.3: Regression lines for clutch size against body length calculated by the baseline model in comparison to the data (points) measured by HALL (1964). Food levels are given in Klett units (overall r^2 = 0.872).

3.3.2 Generalized model

The parameter set obtained by fitting on Hall´s data represented a suitable solution for the description of his data set but seemed to lack generality when compared to results from other studies of *D. galeata*, *D. hyalina* or its hybrid. In particular, the usage of Klett units as a measure of food supply is problematic and difficult to associate with results from analogous investigations. Moreover, a comparison to data on growth and egg production from other publications revealed that: (i) the value for L_0 = 0.35 mm appeared to be very low (e.g. DE MEESTER & WEIDER, 1999), (ii) the measured clutch sizes were uncommonly high (e.g. HÜLSMANN, 2001) and (iii) the initial slope of the growth curves was relatively low (e.g. GIANI, 1991). In order to obtain a more general parameter solution we calibrated the baseline model on a broader basis of experimental data. However, the general functional relationships, i.e. the eqs. 3.3–3.8, were considered to be valid and therefore have been retained for the whole recalibration procedure. Parameter estimation for the generalized model was performed using data of four publications (STICH & LAMPERT, 1984; GLIWICZ & LAMPERT, 1990; GIANI, 1991; VANNI & LAMPERT, 1992), which in total led to the recalibration of the following parameters: b_1, α_{max}, K_α, and β_{min} (Table 3.4). All studies employed to this parameter estimation were using *Scenedesmus acutus* as food algae and mg C L^{-1}as a measure of food quantity. Therefore, the generalized model interprets the input value for food supply as mg C L^{-1} *Scenedesmus acutus*.

For the recalibration of the somatic growth submodel 12 different growth curves

Table 3.4: Parameter estimates of the generalized model; those parameters not shown were equal to the respective values in Table 3.1 and Table 3.3. Model results for somatic growth (r^2 = 0.954, n = 88) and egg production (r^2 = 0.931, n = 35) are in good accordance with observed data (p = significance level).

Parameter	Value	Unit	Standard error	p
Somatic growth				
b_1	$10.89 \cdot 10^{-3}$	d^{-1}	$0.2 \cdot 10^{-3}$	< 0.001
$L_{0,Hall}$	0.35	mm	—*	—*
Egg production				
α_{max}	23.83	eggs	6.39	< 0.001
K_α	0.65	mg C L^{-1}	0.35	< 0.001
β_{min}	-29.28	eggs	2.61	< 0.001

*no free parameter

taken from 4 studies were used (STICH & LAMPERT, 1984; GLIWICZ & LAMPERT, 1990; GIANI, 1991; VANNI & LAMPERT, 1992). Obviously, size of neonates (L_0) varied markedly in these studies and hence it did not seem useful to apply one fixed value of L_0 to all curves. As a solution, we used the value of L_0 as observed in HALL (1964) as a base value (0.35 mm) and included an additive value $\triangle L$ to Eq. 3.3 with $\triangle L = L_{0,observed} - L_{0,Hall}$ where $L_{0,observed}$ is the actual value of the size of neonates as observed in the original growth curve (see also Table 3.5). By setting the body length of an individual at the age t = 0 in the model equal to the size of neonates in the respective experimental study, this approach eliminated the influence of different life histories on the shape of the growth curves. This enabled us to illustrate the influence of temperature and food concentration independently of life history plasticity. Finally, parameter estimation on the 12 growth curves required the recalibration of only one parameter (b_1, value shown in Table 3.4). All other parameters of the somatic growth submodel were kept constant. The recalibrated growth model reproduced the measured growth curves with a high coefficient of determination (r^2 = 0.954, n = 88).

For the recalibration of the submodel of egg production, 10 different experiments taken from 3 studies were used (STICH & LAMPERT, 1984; GLIWICZ & LAMPERT, 1990; VANNI & LAMPERT, 1992). It was necessary to recalibrate all involved parameters (except u_c). An overall parameter estimation was conducted (Table 3.4) and, again, the model results were in good accordance with the measured clutch sizes (r^2 = 0.931, n = 35). A comprehensive description of the complete generalized model specification is given in Table 3.5.

Table 3.5: Generalized model specification; Units of parameters see Tables 3.11 and 3.3

Somatic growth	
$L_t = L_{max} - (L_{max} - 0.35) \cdot e^{-kt} + \triangle L$	$L =$ body length (mm)
with	$t =$ age (d)
$L_{max} = \frac{1.167 \cdot F}{0.537 + F} + 1.42 - 2.397 \cdot k$	$L_{max} =$ maximal body length (mm)
$k = 0.0109 \cdot e^{0.122 \cdot T}$	$\triangle L =$ additive length term (mm)
$\triangle L = L_{0,observed} - 0.35$	$k =$ von Bertalanffy coefficient (d^{-1})
Egg production	$F =$ mg C L^{-1} *Scenedesmus acutus*
$E = \frac{23.83 \cdot F}{0.65 + F} \cdot L - 29.28 \cdot (1 - e^{-1 \cdot F})$	

3.4 Results

3.4.1 Individual based simulation

Population size grew up discontinuously during the simulations due to synchronized hatching of siblings. Nevertheless, the development of population size over large time intervals follows exponential growth (Fig. 3.4). At the beginning of each simulation reproduction was delayed until the starting animal (neonate) has reached maturity (e.g. 6 days at 20°C, 1 mg C L^{-1}; 12 days at 20°C, 0.2 mg C L^{-1}; 29 days at 10°C, 0.2 mg C L^{-1}). One further egg development time after reaching size at first reproduction the first hatchlings were released (e.g. 38 days at 10°C and 0.2 mg C L^{-1}, Fig. 3.4). Population birth rate *b* increased with rising temperature and food concentration (Fig. 3.5). But at food concentrations above approximately 0.4 mg C L^{-1} *Scenedesmus acutus* temperature was the main determinant of population birth rate. At temperatures below 5°C no reproduction was detectable during the simulation period of 60 days. At these temperatures reproduction was limited by slow somatic growth and long egg development time. Nevertheless, a simulation longer than 60 days showed a slight population growth even at this low temperature. Maximal population birth rates calculated in the applied range of temperature and food concentrations were about 0.25 d^{-1}. Increasing food concentration led to higher clutch sizes (Fig. 3.6) and larger maximal body length of the adults (Fig. 3.5) whereas increasing temperature led to faster egg development and somatic growth but also to slightly reduced maximal body length of the adults (Fig. 3.5).

3.4.2 Model applications

Correlation between juvenile somatic growth and population birth rate: Juvenile growth rate *g* of individuals was likewise affected by both, temperature and food concentration and showed a response comparable to population birth rate in the applied range of temperature and food supply (Fig. 3.7 A). However, the effect of food concentration on juvenile growth rate was more pronounced at higher temperatures. Population birth rate was highly correlated with juvenile growth rate (Fig. 3.7 B, $r^2 = 0.95$). However, at very low food concentrations the population birth rate showed some deviations from the calculated regression line (Fig. 3.7 B, open circles). Calculated birth rates at these low food concentrations were lower than estimated from the respective

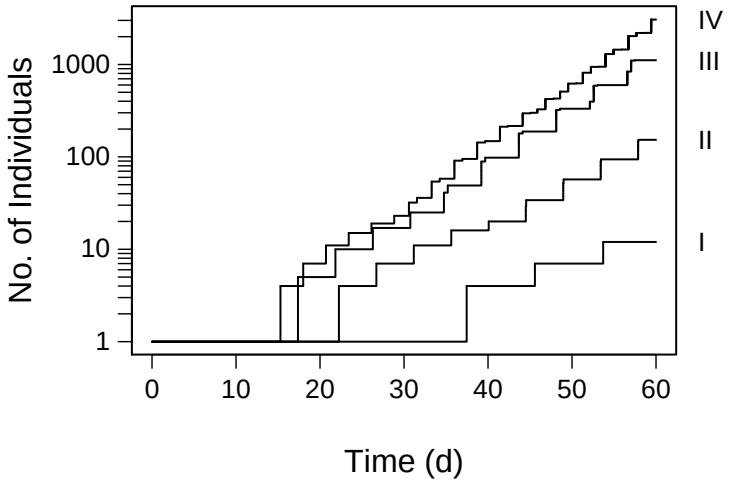

Figure 3.4: Population development in the individual based simulations at different conditions of food concentration and temperature: (I) 10°C, 0.2 mg C L^{-1}; (II) 15°C, 0.2 mg C L^{-1}; (III) 15°C, 0.5 mg C L^{-1}; (IV) 20°C, 0.2 mg C L^{-1}. Due to constant values of temperature, food concentration, size at first reproduction and size of neonates during simulations populations showed synchronized growth.

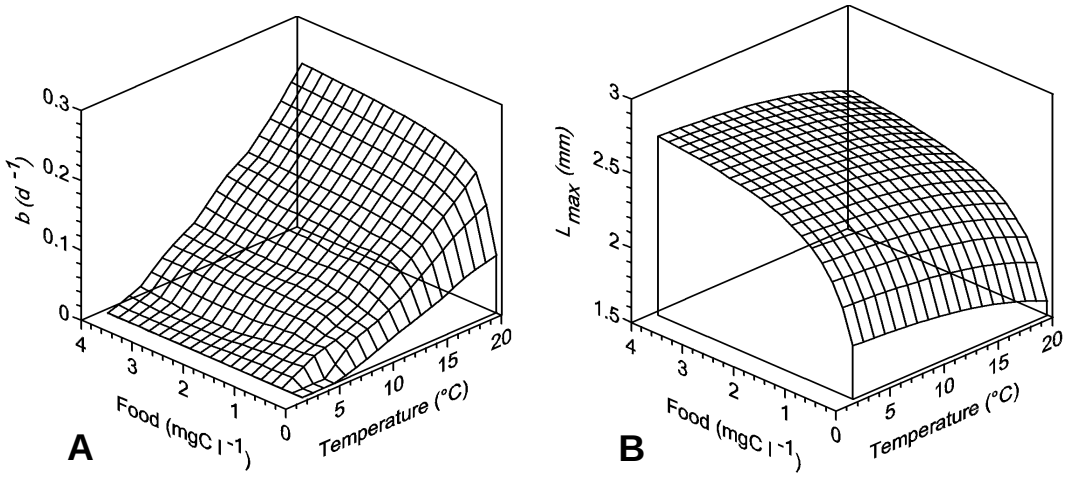

Figure 3.5: (A) Application of the generalized model in an individual based simulation: Population birth rate *b* at different temperature and food conditions as calculated by the individual based model. (B) Theoretical maximal body length calculated by the generalized model for different values of temperature and food concentration.

juvenile growth rate, i.e. at strong food limitation juveniles can still grow distinctly in size although they will hardly start, if ever, to reproduce.

Effects of temperature on population birth rate: The contribution of delayed somatic growth to the overall temperature effects on population birth rate ranged from 33 % to 78 % (Table 3.6) with higher values in the high food scenario. As expected, this contribution increased with decreasing temperature. Thus, besides longer egg development times delayed somatic growth has a considerable influence on population growth due to later maturation. A complex pattern in the temperature reaction norm of population birth rate emerged from these simulation results because several individual level processes interact with each other and this interaction changes with food concentration. The temperature reaction norm of egg development is different from that of population birth rate and this difference is even more pronounced at high food concentrations.

Food-dependent size at first reproduction (SFR): According to the findings about the significant effect of delayed somatic growth on population birth rate, the model also proved clear differences in birth rates between scenarios with an either fixed or food-dependent size at first reproduction (SFR). As expected, a reduction of the SFR at low food concentrations led to higher birth rates due to earlier maturation (Table 3.7). The SFR at the highest food concentration (2.5 $\mathrm{mg\,C\,L^{-1}}$) was larger than the reference SFR in the standard scenario. Surprisingly, this increase in SFR did not lead to reduced birth rates but to even slightly higher values. This can only be understood by taking into account the higher clutch sizes due to larger size of animals. Especially at high food concentrations, individual clutch size strongly increases with body length. Hence, the benefits from an elevated clutch size could compensate the costs arising from later maturation.

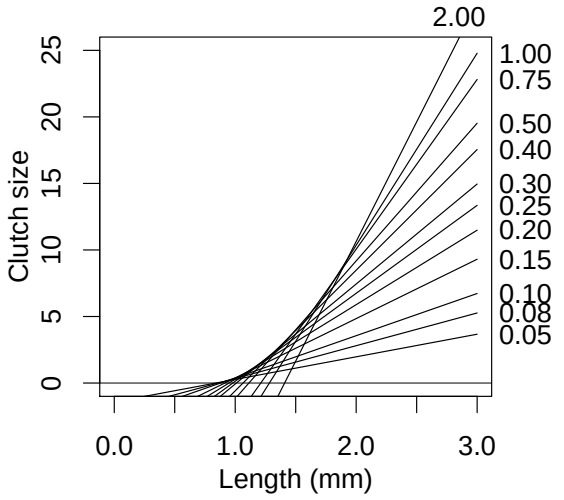

Figure 3.6: Relationship between individual body length and clutch size at different food concentrations as calculated by the generalized model. Values at the upper end of each line indicate the respective food concentration (mg C L^{-1}).

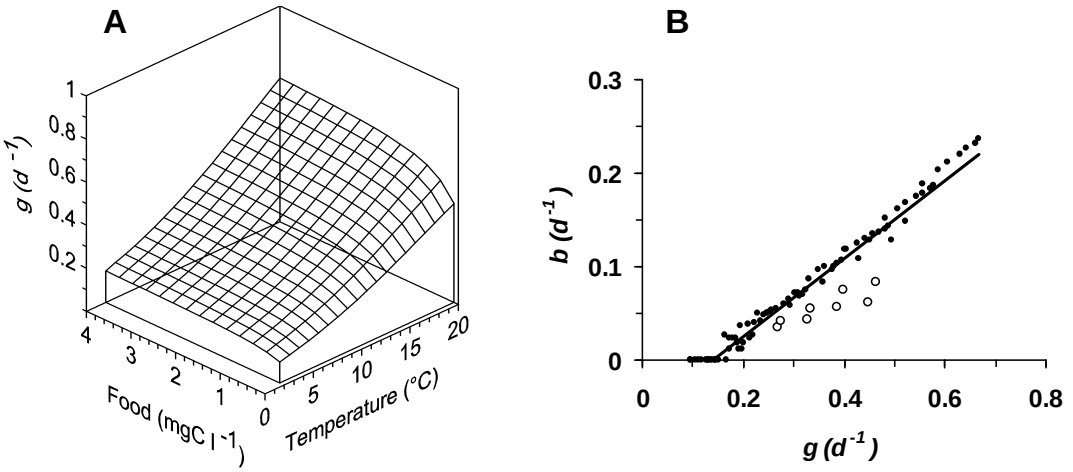

Figure 3.7: (A) Juvenile somatic growth rate g (d^{-1}) calculated by the generalized model. The same ranges of temperature and food concentration were applied as in Fig. 3.5. (B) Regression analysis of population birth rate b (d^{-1}, open circles and points) and juvenile growth rate g (d^{-1}). Birth rate is highly correlated with juvenile growth rate ($b = 0.416 \cdot g - 0.06$, $r^2 = 0.95$). Open circles mark those rates calculated at temperatures > 10°C and food supply < 0.2 mg C L^{-1}. Regression and correlation analysis were conducted by using all data points.

Table 3.6: Population birth rates b at different temperatures and two food concentrations: a limiting food concentration (0.1 mg C L^{-1}) and a non-limiting food concentration (0.75 mg C L^{-1}). Birth rates of standard scenarios (Standard: somatic growth and egg development depend on ambient temperature according to the generalized model) are compared with the manipulated scenario (Manipulated: somatic growth depends on ambient temperature but egg development time is fixed at a value that corresponds to egg development at 20°C; see Section 3.2.3 for details). Normalized birth rates are given as percentage of the birth rate at 20°C. The effect of delayed somatic growth at a given temperature was quantified as relative birth rate reduction (in relation to birth rate at 20°C) in the manipulated scenario divided by the relative birth rate reduction in the standard scenario. For comparison, the rate of egg development (e) according to BOTTRELL *et al.* (1976) is given for the specified temperatures (absolute values and percentages relative to egg development at 20°C). Egg development rate was calculated as the inverse of egg development time.

			Food = 0.1 mg C L^{-1}					Food = 0.75 mg C L^{-1}				
	Rate of egg development		Standard		Manipulated			Standard		Manipulated		
T (°C)	e (d^{-1})	e (%)	b (d^{-1})	b (%)	b (d^{-1})	b (%)	Effect (%)	b (d^{-1})	b (%)	b (d^{-1})	b (%)	Effect (%)
5.0	0.057	15	0.000	0	0.000	0	—	0.023	11	0.066	32	76.3
7.5	0.086	23	0.012	14	0.037	44	64.7	0.040	20	0.076	37	78.2
10.0	0.124	33	0.027	32	0.049	59	60.1	0.060	30	0.107	53	67.2
12.5	0.170	46	0.041	50	0.055	67	67.2	0.097	48	0.132	65	67.7
15.0	0.226	61	0.055	67	0.070	85	44.4	0.125	62	0.155	76	62.2
17.5	0.293	79	0.073	89	0.080	96	33.7	0.162	80	0.181	89	54.0
20.0	0.372	100	0.083	100	0.083	100	—	0.203	100	0.203	100	—

Table 3.7: Population birth rates at different food concentrations with either food-dependent size at first reproduction (SFR) according to BOERSMA & VIJVERBERG (1995b) (left panel) or a fixed SFR (right panel).

	SFR according to BOERSMA & VIJVERBERG (1995b)		Fixed SFR (independent of food)	
Food (mg C L^{-1})	SFR (mm)	b (d^{-1})	SFR (mm)	b (d^{-1})
0.13	1.3	0.107	1.5	0.085
0.25	1.4	0.132	1.5	0.118
0.50	1.5	0.154	1.5	0.154
2.50	1.6	0.182	1.5	0.178

Costs of diel vertical migration: The example of diel vertical migration of *Daphnia hyalina* in Lake Constance is characterized by very different environmental conditions of the animals during day (mean population depth at 30m, 6°C, 0.07 mg C L^{-1}) and night (mean population depth at 10m, 14°C, 0.16 mg C L^{-1}). By assuming all individuals staying in the epilimnion for 24h the population would realize a birth rate of 0.062 d^{-1}.At conditions of vertical migration (light:dark = 14h:10h), this birth rate is reduced to 0.026 d^{-1}. This reduction of about 40% reflects the costs associated with diel vertical migration at these environmental conditions.

3.5 Discussion

The multiple regression model presented consists of a relatively small set of functions, which describe the effects of food concentration and temperature on somatic growth and reproduction in *Daphnia*. The model is purely empirical, but applicable over broad ranges of food (0.1 - 4 mg C L^{-1}) and temperature (2 - 20°C). Altogether, nine parameters were fitted in the multiple regression approach (parameter u_c does not provide a degree of freedom). These parameters are constants and should be valid without recalibration in situations within the specified ranges of temperature and food supply. Two further life-history parameters (size of neonates, size at first reproduction) were needed in order to characterize complete individual daphnid life history.

In experimental studies, variability in individual somatic growth and egg production is observed even at conditions of constant temperature and food and can be attributed to the plasticity of cladoceran life histories (e.g. DE MEESTER & WEIDER, 1999). However, it was an intended aim of this study to disregard the processes in-

volved herein and consequently no investigations involving kairomones in the experimental designs were used for the calibration. Existing differences in the daphnid life histories of the used investigations might be associated with clonal differences (DE MEESTER & WEIDER, 1999) or maternal effects (LAMPERT, 1993b). As there is still a lack of any quantitative understanding of cladoceran life history plasticity only pragmatic approaches were available. However, with regard to the investigations of LAMPERT (1993b) concerning maternal effects of *Daphnia*, the usage of additive terms ($\triangle L$) as done in this study might be a suitable approach. Additionally, such effects could be integrated into the model by linking the size of a neonate to the size of the mother or their physiological state and further linking the size at first reproduction of an individual to its own size at birth and the presence of kairomones. This would mean that size at first reproduction is not a constant value applied to all individuals in a simulation but that size at first reproduction differs between individuals.

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Not only the individual growth but also the population birth rates calculated by the model are in accordance with published values (BOERSMA & VIJVERBERG, 1995b; SPAAK *et al.*, 2000; WEBER, 2001). Nevertheless, population birth rates generally showed certain variability over a relatively wide range and other investigations re-

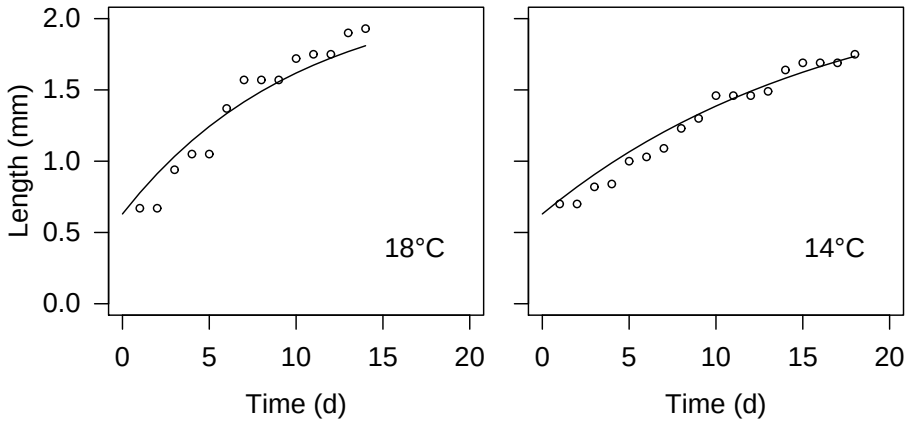

Figure 3.8: Validation of the model on somatic growth data of *Daphnia galeata* × *hyalina* taken from DOKSAETER & VIJVERBERG (2001). Experiments were conducted at 1 mg C L^{-1} *S. obliquus* and at two temperatures (14°C and 18°C)

vealed higher values (e.g. BOERSMA & VIJVERBERG, 1995a; DE MEESTER & WEIDER, 1999). Clonal differences, the demography of the start population, different values for size at first reproduction or varying experimental set-ups (e.g. varying food quality) might account for these discrepancies. The model predicted a maximal body length an individual could ever reach under food-saturated conditions of 2.7 mm (at 10°C), which is in agreement with (FLÖSSNER, 2000) for *Daphnia galeata* or *Daphnia hyalina*. Furthermore, the calculated values for age at first reproduction at different temperatures and food concentrations agree well with observed values (e.g. DE MEESTER & WEIDER, 1999). Application of the model to life-history data that have not been used for the development of the model as well showed good agreement between model outputs and measurements (Fig. 3.8).

Somatic growth, egg production and egg development time of individual *Daphnia* were simulated by the IBM under different conditions of temperature and food. The individual based simulation hereby acts as an integrator of these three sub-processes and provides the possibility to assign the effects of temperature and food to the population level. The population birth rate *b* was strongly affected by temperature through its control of egg development time and initial somatic growth. Nevertheless, food had a considerable influence on the population birth rate if its concentration fell below a critical value of approximately 0.4 mg C L^{-1}. Except at those low food levels pop-

ulation birth rate and juvenile growth rate g were highly correlated because of their predominant control through temperature. Furthermore, if temperature is kept constant, the juvenile growth rate and population birth rate were also correlated due to their sole dependence on food concentration. Hence, the model supported the results of LAMPERT & TRUBETSKOVA (1996) who found a good correlation between juvenile growth rate and population birth rate. However, at very low food concentrations population birth rate was lower than expected according to the calculated regression line (Fig. 3.7). One reason for this deviation is the usage of a fixed length-weight relationship. URABE & WATANABE (1991) showed that individuals of *D. galeata* grown under different food supplies differed markedly in their length-weight relationships, i.e. individuals of the same length grown at high food supply were heavier than individuals grown under food limitation. This effect would move the deviating points closer to the regression line in Fig. 3.7. But another reason for this deviation is probably the fact that at very low food concentrations initial somatic growth can be performed from the energy storage of the egg whereas population birth rate will be substantially limited due to very small clutch sizes. Although the application of one fixed length-weight relationship is problematic, the energy storage effect might be important as well, as it is predicted by KOOIJMAN (2000) in his concept of dynamic energy budget models.

The application of a food dependent size at first reproduction (SFR) showed a significant influence on population birth rate in comparison to the standard scenario with a fixed SFR (see Table 3.7). Up to now, most individual level modelling approaches to *Daphnia* applied a fixed SFR (e.g. GURNEY *et al.*, 1990; HALLAM *et al.*, 1990; KOOIJMAN, 2000). However, this study shows the great importance of food dependent SFR at the population level. Even more, the model output enabled a quantitative view on the adaptive value of this variable SFR because observed SFR in BOERSMA & VIJVERBERG (1995b) produced in the simulations always higher birth rates than in simulations with a fixed SFR. At low food concentrations a reduced SFR is adaptive because of earlier maturation and at high food concentrations a larger SFR is adaptive due to larger clutch size. Hence, further model approaches should include a food dependent SFR. Another point that has to be checked in further applications is the effect of food-dependent size of neonates on population birth rate (MCCAULEY *et al.*, 1990a).

In the model specification, increased food concentrations led to an increasing slope

of the body length - clutch size relationship (see Eq. 3.6) whereas the intercept of this relation decreased (see Eq. 3.8). If these lines are compared over a range of food concentrations an obvious increase of the intercept with the x-axis (clutch size is zero) with increasing food concentrations can be observed (see Fig. 3.6). Further, if this intersecting point with the x-axis is interpreted as a kind of physiological size at first reproduction, we found an increasing size at first reproduction with an increasing food concentration as proven by experimental works (e.g. BOERSMA & VIJVERBERG, 1995b; GIEBELHAUSEN & LAMPERT, 2001). Moreover, BOERSMA *et al.* (1996) correlated maximal body size and size at first reproduction and the observed ratio between size at first reproduction and maximal body size they have observed was a value averaging 0.62. The mean ratio between physiological size at first reproduction and maximal body size in the simulations shown above was 0.56, which is comparable with the observations. This accordance is remarkable because the ratio between size at first reproduction and maximal body size was no criterion of the parameter fitting procedure.

The effects of food and temperature on population growth will be particularly important for populations performing diel vertical migration (DVM). As this model scenario showed, migrating populations suffer reduced birth rates because of lower temperatures and food concentrations during the day. Due to the dominant influence of temperature on population growth we should expect the reduction of temperature as the main limiting factor of the gross population growth rate of a migrating population. Indeed, this model indication was found earlier by laboratory investigations (DAWIDOWICZ, 1994; LOOSE & DAWIDOWICZ, 1994) that proved the temperature reduction, and not food reduction, as the main cause of costs of DVM. Moreover, if the model predictions are sound one should expect an exception at very low food concentrations (below approximately 0.4 $\mathrm{mg\,C\,L^{-1}}$) where a further lowering of food supply during DVM is becoming more costly. Indeed, JOHNSON & JACOBSON (1987) observed a lack of DVM under low food concentrations in a mesocosm experiment and FLIK & RINGELBERG (1993) found comparable results in a field study. With respect to the model results this pattern must be interpreted as the avoidance of elevated costs. Besides, it has to be considered that this critical food concentration could vary *in situ* due to different food quality.

The development of a given population over time is hard to describe when an approach is purely focused on the population level (DE ROOS & PERSSON, 2001). There

are several underlying individual level processes that interact in a complex manner and together result in what is called population dynamics. Therefore, model approaches to population dynamics should provide a structure to take these individual level processes into account — at least when relatively high-organized organisms that display particular life-cycles are involved. As shown in the second model application (effects of temperature on population birth rate), classical population level approaches are not able to incorporate this complexity. Therefore, it might become necessary for many model applications in applied ecology (e.g. water quality management models), which should provide quantitative and reliable insights into a given problem, to adapt to other model approaches. These approaches have to incorporate distinct individual level processes and have to include information about population demography.

With this multiple regression model a simple-to-use approach for the modelling of growth and reproduction of *Daphnia* is presented. Effects of food concentration and temperature could be quantitatively described and individual based simulations resulted in reasonable individual as well as population dynamics. This model can be applied to detailed simulations of *Daphnia* population dynamics under realistic environmental conditions and represents a useful tool to empirical scientists who want to interpret their findings by means of a model.

4 A mechanistical approach to individual life-history and population dynamics of *Daphnia* by a bioenergetic model[1]

Abstract

A model framework for the simulation of growth and reproduction of *Daphnia* at varying conditions of food concentration and temperature is presented. The core of the framework consists of an individual level model that simulates allocation of assimilated carbon into somatic growth, maintenance costs and reproduction on the basis of a closed carbon budget. A fixed percentage of assimilated carbon is allocated into somatic growth and maintenance costs. Special physiological adaptations in energy acquisition and usage allow realistic model performance even at very low food concentrations close to minimal food requirements. All model parameters are based on physiological measures taken from the literature. Model outputs were thoroughly validated on data from a life-table experiment with *Daphnia galeata*. For the first time, a successful model validation was performed at such low food concentrations. The escalator boxcar train (EBT) technique was used to integrate this individual level model into a stage-structured population model. In advance to previous applications of the EBT to *Daphnia* an additional clutch compartment was included into the model structure that accounts for the characteristic time delay between egg deposition and hatching in cladocerans. By linking two levels of biological organization, this model approach represents a comprehensive framework for studying *Daphnia* both at laboratory conditions and in the field. Outputs of the model were

[1] Main results of this chapter have been published in RINKE, K. & J. VIJVERBERG, 2005: A mechanistical model approach to evaluate the effect of temperature and food concentration on individual life-history and population dynamics of *Daphnia*. Ecological Modelling 186, 326-344.

compared with predictions by two other models having analogous parameterization: (i) another individual level model of *Daphnia* (Kooijman-Metz model) and (ii) a classical unstructured population model. In contrast to the *Daphnia* model presented here, the Kooijman-Metz model lacks the structure to account for the optimization of energy acquisition and maintenance requirements by individual daphnids. The unstructured population model showed different patterns of population dynamics that were not in concordance with typical patterns observed in the field. It is concluded that the model provides a comprehensive tool for the simulation of growth and reproduction of *Daphnia* and corresponding population dynamics.

4.1 Introduction

In the temperate region, *Daphnia* species are able to control algal blooms and are preferred food items for zooplanktivorous fish; they are key-species in most freshwater aquatic food webs and model organisms in aquatic ecology (STERNER, 1989; CARPENTER & KITCHELL, 1993). Therefore, it is not surprising that there is a long tradition of modelling individual and population level dynamics of *Daphnia*. Nowadays, we have an enormous diversity of models regarding model aim, subject, and methodology. Population level models (e.g. BENNDORF & HORN, 1985; SCAVIA *et al.*, 1988; NISBET *et al.*, 1991; SCHEFFER *et al.*, 2000; OMLIN *et al.*, 2001), sometimes integrated into whole lake models, are mostly dealing with basic aspects of resource limited growth or predator-prey dynamics whereas more recently developed approaches like structured population models (NISBET *et al.*, 1989; DE ROOS *et al.*, 1992; MCCAULEY *et al.*, 1996, 1999) or individual based models (GURNEY *et al.*, 1990; MOOIJ & BOERSMA, 1996; RINKE & PETZOLDT, 2003) are also capable of reflecting demographic effects and size dependent processes.

The use of individual-based or size-structured models is important because life history traits and metabolic rates are generally related to body size. In *Daphnia*, ingestion and respiration rates are strongly influenced by individual size (ARMITAGE & LEI, 1979; KNOECHEL & HOLTBY, 1986; LYNCH *et al.*, 1986) leading to size dependent net production rates (LYNCH *et al.*, 1986; URABE & WATANABE, 1991) and size related fecundity (e.g. HALL, 1964). Furthermore, reproduction in *Daphnia* only starts at a distinct body size. Therefore, a distinct proportion of the population, i.e. juveniles, does not participate in reproduction - a fact that the classical non-structured popula-

tion models do not take into account. Size is also important in population dynamics owing to close relationships between body size and related ecological processes (e.g. size selective predation, starvation resistance, success of predator avoidance; PETERS, 1983) and, therefore, reveals an interplay between the physiological properties of an individual organism and community structure. In cladoceran populations, size structure is closely linked to age structure, and thus to demography. Some patterns in population dynamics of *Daphnia* are attributed to demographic effects. For instance, cycles in *Daphnia* density as often observed in mesocosms and in the field without any influence of predation are mostly consequences of the life cycle of *Daphnia* and the accompanying demography of the population (SLOBODKIN, 1954; MCCAULEY & MURDOCH, 1987; MCCAULEY *et al.*, 1999).

Existing individual based and stage-structured population models commonly use concepts based on energy allocation rules. Most studies are focused on resource dynamics or predator-prey cycles in laboratory experiments at constant temperature conditions (mostly 20°C). In a basal work of MCCAULEY *et al.* (1990b) and GURNEY *et al.* (1990) this approach was used to study in *Daphnia pulex* the allocation of assimilated energy into maintenance, growth, and reproduction. Their approach is convincing because (i) the closed energy budget represents a detailed mechanistic explanation of previously observed life history phenomena, (ii) all physiological rates in the model are based on measurements in laboratory experiments, and (iii) the model provides a framework that opens the possibility to bridge over two levels of biological organization (individual level, population level; see DE ROOS *et al.*, 1997). Almost in parallel, Kooijman and colleagues (KOOIJMAN & METZ, 1984; KOOIJMAN, 1986) developed the concept of dynamic energy budget models (DEB-models), which is much more than a growth model of *Daphnia* but a broadly applicable framework of individual metabolic organization (KOOIJMAN, 2000). In contrast to McCauley's and Gurney's idea, he introduced generalized assumptions, e.g. about allometric scaling relationships and principal energy allocation rules (κ-rule) that made his approach mathematically more tractable (KOOIJMAN, 2001). In contrast to the McCauley/Gurney approach, DEB-models follow von Bertalanffy growth (VON BERTALANFFY, 1957). Another novelty in Kooijman's approach is the introduction of a reserve compartment as additional state variable.

Both models, the Kooijman and the McCauley/Gurney modelling approach, show in comparison clear differences although they are both based on energy allocation

rules. In the McCauley/Gurney-model the commitment of energy includes complex kinetics making a further analytical evaluation of the model virtually impossible. Model behavior can only be investigated by numerical techniques (i.e. simulation surveys) as shown by DE ROOS *et al.* (1997). They compared model predictions with observations on *Daphnia* populations in the laboratory and showed substantial deviations between model predictions and the observed *Daphnia* population dynamics, which were attributed to erroneous scaling relationships of physiological rates with body size. The Kooijman modelling approach offers three important advantages compared with the McCauley/Gurney approach: (i) the model structure provides analytical solutions that opens his model framework to comprehensive mathematical evaluation (DE ROOS, 1997; KOOIJMAN, 2000), (ii) the model is based upon general assumptions about scaling relationships and energy allocation rules which solve the scaling problems of physiological rates mentioned above, and (iii) the framework contains a defined structure for the incorporation of temperature as a driving factor (KOOIJMAN, 1986, 2000).

For this approach, a new model structure was used that represents a combination of the two model approaches presented by McCauley/Gurney and Kooijman. By following KOOIJMAN (1986) the scaling relationships between physiological rates and body size and the basic energy allocation rules (κ-rule) of DEB-models have been adopted in order to open the model for possible mathematical evaluation. The scaling of physiological rates with ambient temperature was, as well, applied as suggested for the DEB-models (KOOIJMAN, 2000). However, regarding principal energy channelling the approaches of MCCAULEY *et al.* (1990b) and GURNEY *et al.* (1990) were followed and assimilated energy were immediately allocated to growth and reproduction without the use of a reserve compartment. In order to assign the outcomes of the individual level model to the population level the model was further integrated into the Escalator Boxcar Train (EBT) framework (DE ROOS *et al.*, 1992, 1997). This framework allows the inclusion of individual level models into a stage-structured population model, where the population is divided into distinct age-classes that are characterized by individual level properties (e.g. length, age, ingestion rate, ...).

The main purpose of this study was to develop a simulation framework that allows the quantitative simulation of *Daphnia* under varying food supply and temperature. An individual level model based on energy allocation rules, rigorously validated on experimental data, constitutes the core of this approach. In order to allow an efficient

simulation on the population level the individual level model was integrated into a physiologically structured population model.

4.2 Methods

4.2.1 Life table experiments (conducted by J. Vijverberg[2])

The experiment was performed with one clone (GAL21) of *Daphnia galeata* from Tjeukemeer, The Netherlands. This is a well-established laboratory clone from the Netherlands Institute of Ecology (NIOO-KNAW) of *D. galeata* (SCHWENK *et al.*, 2000), which was used in life history studies before (e.g. REPKA *et al.*, 1998, 1999) and has proven to be a representative clone in terms of life history parameters.

Experimental animals were kept individually in 100 ml glass test tubes at 17°C and a light: dark regime of 16:8 h, as described in detail by BOERSMA & VIJVERBERG (1994b). Log-phase cells of *Scenedesmus obliquus* grown in chemostats were used as food. Prior to the start of the experiment the animals were adapted to laboratory conditions at a food concentration of 0.5 mg C L^{-1}, a food concentration that is well above the Incipient Limiting Level for *Daphnia galeata* (LAMPERT, 1987). The culture was started with one female, the newborn from the second to the third brood produced by the third generation were used in the experiment. Five different food concentrations were tested: 0.04, 0.11, 0.18, 0.25 and 0.50 mg C L^{-1}. Each food treatment consisted of 5 replicates starting with a newborn not older than 24 h.

The animals were inspected and transferred to clean tubes with fresh medium every day. Length growth (length versus time), duration times of instars and eggs, fecundity (number of eggs), and age and size at first reproductions were noted. Mortality was in the range of 1-2% d^{-1}, which is generally the case in well-designed *Daphnia* cultures (VIJVERBERG, 1989). Life table experiments were continued until the animals reached the 3rd adult instar.

4.2.2 Parameterization and data management

Information from the literature about significant physiological properties of *Daphnia galeata* were included in the model structure. Somatic growth, gonad production and

[2] All experimental work of this chapter was performed by Dr. Jacobus Vijverberg, Netherlands Institute of Ecology, Centre for Limnology, Nieuwersluis, and kindly provided for modelling purposes.

assimilation were expressed in terms of carbon mass per day. All those experimental studies of which results were used for parameterization of physiological processes were conducted at 20°C (reference temperature) and thus could be used without *a priori* temperature correction. Investigations generally used small green algae (*Chlamydomonas, Scenedesmus*) as food that are readily ingestible and properly assimilated by *Daphnia* (URABE & WATANABE, 1991; HEIN *et al.*, 1993).

Size of the neonates (*SON*) in the model system was based on the observed neonate lengths in the life-history experiments (arithmetic mean). Energy allocation to gonad mass is converted into eggs at the end of the molting cycle by dividing accumulated gonad mass by the carbon investment per egg. In *Daphnia*, deposition of eggs only occurs directly after molting and eggs are kept within the brood chamber until the next molt when they are released as neonates. Thus, the current clutch size (of adults instar $\#\,n+1$) represents the egg production over the previous molting cycle (of adults instar $\#\,n$).

4.2.3 Technical information about simulation tools

Data analysis and all simulations were performed using the **R** language (IHAKA & GENTLEMAN, 1996, free available at `http://cran.r-project.org/`). The availability of numerical solvers for ordinary differential equations, modern statistical methods, and a graphical user interface within one environment makes it particularly suited for applications in ecological modelling, as pointed out by PETZOLDT (2003). For numerical integration of the differential equations a fourth order Runge-Kutta algorithm was used with a time step of 0.1 d. Requests for all used R-scripts are welcome.

4.3 Model

4.3.1 Individual level

In individual level models, it is of crucial importance how certain rates scale with individual body length. Length dependence of such rates like ingestion or respiration rate is well studied in *Daphnia* but the published scaling powers differ widely (e.g. compare LYNCH *et al.*, 1986; URABE & WATANABE, 1990, 1991). Hence, some assumptions about appropriate scaling relationships are necessary to receive a unifying

solution for the scaling problem. This can be provided by general DEB-theory (see KOOIJMAN, 2000). Assuming that the individual does not change its shape during growth we can expect weight (W) to be proportional to cubic length (L, Eq. 4.1) leading to the length-weight relationship given by Eq. (4.2). Accordingly, body surface area (S) should be proportional to squared body length and to weight to the power of 2/3, respectively (Eq. 4.3).

$$W \propto L^3 \tag{4.1}$$

$$W = aL^3 \tag{4.2}$$

$$S \propto L^2 \propto W^{\frac{2}{3}} \tag{4.3}$$

For *Daphnia galeata* a large number of length-weight relationships are available that altogether show a considerable variability in their parameters. After careful examination of existing length-weight regressions those from URABE & WATANABE (1991) and LYNCH *et al.* (1986) were considered as most representative for *D. galeata* and parameter a was adjusted to a value of 1.6 corresponding to their regressions (parameter dimensions are provided in Table 4.1).

Simulated state variables of individual *Daphnia* are body weight (W) and accumulated carbon in gonads (R). Assimilated carbon is allocated to gonad mass, somatic mass and maintenance costs (Fig. 4.1). The carbon flow is described by the central balance equation: assimilation rate (A) equals to the sum of maintenance rate (M), somatic growth rate (dW/dt), and reproductive rate (dR/dt):

$$A = M + \frac{dW}{dt} + \frac{dR}{dt} \tag{4.4}$$

A fixed fraction of assimilate (κ) is allocated into somatic growth and maintenance (κ-rule, see KOOIJMAN, 2001). Thus, somatic growth rate becomes:

$$\frac{dW}{dt} = \kappa A - M \tag{4.5}$$

KOOIJMAN (2000) provided estimates of κ for different species and gave a value of approximately $1/3$ for *Daphnia*. In the present study, a value of 0.35 was applied. The

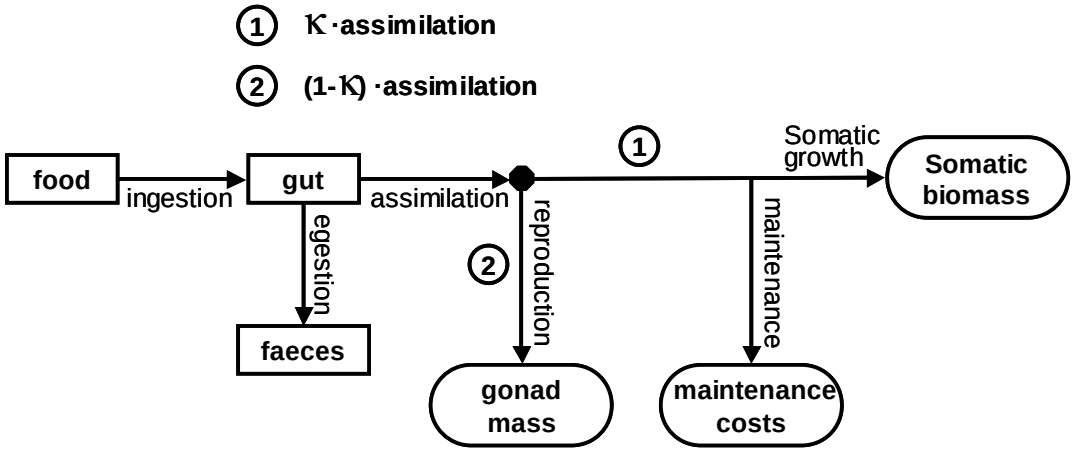

Figure 4.1: Flow chart of energy allocation in *Daphnia*. The compartments indicate carbon pools and next to arrows relevant processes are declared. According to DEB-theory (κ-rule) a fixed fraction of assimilate is allocated into somatic growth and maintenance (κ) and the remaining assimilate (1-κ) is committed to reproduction and maturation.

remaining assimilate $(1-\kappa)$ is channelled into gonad mass leading to the reproductive rate:

$$\frac{dR}{dt} = (1-\kappa)A \tag{4.6}$$

The effect of temperature (T, in Kelvin) on physiological rates was modelled with an Arrhenius scale (KOOIJMAN, 2000):

$$f(T) = e^{\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)} \tag{4.7}$$

Here T_A refers to the Arrhenius temperature and T_{ref} stands for the reference temperature. KOOIJMAN (2000) stated an Arrhenius temperature of 6400 K for *Daphnia*. Reference temperature is 293 K (i.e. 20°C) representing the temperature at which physiological rates had been measured. For temperatures T above T_{ref}, the temperature correction term will be $f(T) > 1$ and, accordingly, for $T < T_{ref}$ vice versa. If ambient temperature T equals reference temperature (293 K) the temperature correction factor $f(T)$ equals one.

Ingestion rate (I) scales with surface area and according to Eq. (4.3) we can as-

sume that:

$$I = p_{ing} W^{\frac{2}{3}} f(F) f(T) \tag{4.8}$$

By following the measurements of URABE & WATANABE (1991) parameter p_{ing} was set to a value of 5.02. The term $f(F)$ corresponds to the functional response in respect to food concentration F and was modelled with a Holling II model (Eq. 4.9). The half saturation constant k_F was found to be 0.164 mg C L^{-1} according to MUCK & LAMPERT (1984).

$$f(F) = \frac{F}{F + k_F} \tag{4.9}$$

Table 4.1: List of model parameters

Parameter	Description	Value	Unit	References
a	Length-weight relationship	1.6	μg C mm^{-3}	a, b
κ	Energy allocation factor	0.35	dimensionless	c
T_A	Arrhenius temperature	6400	K	c
T_{ref}	Reference temperature	293	K	this study
p_{ing}	Ingestion factor	5.02	μg C μg $C^{-\frac{2}{3}}$ d^{-1}	a
k_F	Half saturation coefficient	0.164	mg C L^{-1}	d
$m_{F,max}$	Max. respiration rate	0.3	d^{-1}	b, f
$m_{F,min}$	Min. respiration rate	0.15	d^{-1}	e, f
$E_{A,max}$	Max. assimilation efficiency	0.9	dimensionless	a, g
$E_{A,min}$	Min. assimilation efficiency	0.5	dimensionless	a, g
c_E	Carbon investment per egg	1.3	μg C egg^{-1}	this study
SAM	Size at maturity	1.2	mm	this study
SON	Size of neonates	0.65	mm	this study
$bottrell.a$	Egg development time	3.3956	dimensionless	h
$bottrell.b$	Egg development time	0.2193	dimensionless	h
$bottrell.c$	Egg development time	-0.3414	dimensionless	h
d_b	Background mortality rate	0.05	d^{-1}	i
d_s	Mortality at strong starvation	0.35	d^{-1}	j
p_m	Critical weight factor	0.6	dimensionless	a,f
n	Lifespan	25	d	i

References are: (a) URABE & WATANABE (1991); (b) LYNCH *et al.* (1986); (c) KOOIJMAN (2000); (d) MUCK & LAMPERT (1984); (e) BOHRER & LAMPERT (1988); (f) URABE & WATANABE (1990); (g) PORTER *et al.* (1982); (h) BOTTRELL *et al.* (1976); (i) HÜLSMANN & VOIGT (2002); and (j) ROHRLACK *et al.* (1999a).

Ingested food is assimilated with a certain efficiency (E_A, Eq. 4.10). DEB-theory generally assumes constant assimilation efficiency. However, there is empirical evidence that assimilation efficiency depends on food concentration. From a mechanistical view one can assume assimilation efficiency to be a function of gut residence time leading to high efficiencies at low food and low efficiencies at high food (Eq. 4.11):

$$A = I \cdot E_A \tag{4.10}$$

$$E_A = E_{A,max} - (E_{A,max} - E_{A,min})\, f(F) \tag{4.11}$$

Maximal assimilation efficiency $E_{A,max}$ was found to be up to 0.9 and minimal assimilation efficiency $E_{A,min}$ was set to 0.5 (PORTER *et al.*, 1982; URABE & WATANABE, 1991). High assimilation efficiencies at low food concentrations increase individual ability to cope with food shortage.

Maintenance rate (M) represents the basal energy requirement of an individual (e.g. to bear homeostasis, cell renewal, molting) excluding those energetic costs arising from growth, reproduction or maturation. We assumed maintenance rate to be proportional to body volume, i.e. M scales with cubic length, respectively, with body weight (Eq. 4.12; see KOOIJMAN, 2000). However, empirical studies of *Daphnia* showed that the maintenance coefficient m_F is not a constant but increases with food supply due to the costs arising from specific dynamic action (BOHRER & LAMPERT, 1988). Therefore, maintenance coefficient was defined as a function of food concentration F (Eq. 4.13).

$$M = m_F W\, f(T) \tag{4.12}$$

$$m_F = m_{F,min} + (m_{F,max} - m_{F,min})\, f(F) \tag{4.13}$$

The direct measurement of maintenance rate is difficult and usually approximated via measurement of the respiration rate. Such an approximation is probably not completely correct, e.g moulting costs (i.e. periodical loss of chitine carapax) that accounts for a carbon loss of approximately 5-10 % per day (LYNCH, 1989) are not included in the estimates. However, after examination of the measurements conducted by LYNCH *et al.* (1986) and URABE & WATANABE (1990) maximal maintenance coefficient was set to a value of 0.30 d^{-1}. This maximal maintenance coefficient is significantly reduced under food shortage and observed reductions are up to 50 % if no food is available (BOHRER & LAMPERT, 1988; URABE & WATANABE, 1990). Therefore, a

minimal maintenance coefficient of $0.15\,\mathrm{d}^{-1}$ was assumed that also agrees with the observations by LAMPERT & MUCK (1985)

Reproduction in *Daphnia* strongly depends on body size. At a certain body-size the daphnid becomes adult and from this size onwards at each instar a certain amount of assimilated carbon is allocated into reproduction. Unfortunately, there is no exact definition of the term 'size at maturity' and authors have used it in different ways[3] (compare MACHÁČEK, 1991; EBERT, 1992; STIBOR & LAMPERT, 1993). In this study, size at maturity (*SAM*) is defined as the size at which gonads are becoming ripe and immature eggs can be distinguished inside the ovaries for the first time, and size at first reproduction (*SFR*) as the size of the instar stage at which eggs are deposited in the brood chamber for the first time. According to this definition, *SAM* represents the size of the first adult instar, and *SFR* the size of the second adult instar.

In the present study, energy allocation to reproduction starts at *SAM* in the first adult instar. The life-history data used in this study indicated a *SAM* of 1.2 mm that was independent of food concentration. Juveniles whose size is below *SAM* cannot produce eggs and the energy delivered by reproductive rate is used for maturation (KOOIJMAN, 2001). According to DEB-theory, juveniles become more complex during growth, e.g. by development of new organs (reproductive machinery) and by developing more complex regulation systems (KOOIJMAN, 2000). Moreover, carbon investment into maturation during juvenile stage is measurable in terms of yolk production (MCKEE & EBERT, 1996; STIBOR, 2002). Adults increase in size, but not in complexity. In adults, the clutch size (E) at the end of a molting cycle becomes accumulated carbon in the gonads (R, calculated as integral of Eq. 4.6 over one molting cycle) divided by the carbon investment per egg (c_E, Eq. 4.14).

$$E = \frac{R}{c_E} \tag{4.14}$$

The conversion of accumulated carbon in the gonads into eggs is related with overheads that arise from costs of maintaining the state of maturity and the conversion of assimilates into eggs itself (KOOIJMAN, 2000, 2001). Because direct empirical information about these overheads is not available the same percentage of metabolic overheads as for the somatic biomass has been applied. On basis of this, it was as-

[3] Some authors define size at maturity phenomenologically as the size at first occurrence of eggs in the brood chamber and others prefer a rather physiological definition, i.e. when yolk production has started and eggs are prepared for spawning within the gonads.

sumed that the carbon investment per egg is 30 % higher than the measured carbon content of the eggs. Mean carbon content per egg has been measured by a number of investigators, which found egg carbon content in a rather broad range averaging a value of about 1.0 µg C (e.g. compare BOERSMA, 1995; GUISANDE & GLIWICZ, 1992). Therefore, carbon investment per egg was estimated to be 1.3 µg C egg^{-1}.

Size of neonates (*SON*) released by the mother after egg development time was estimated from the life-history experiment and set to 0.65 mm. Temperature dependent egg development time D was calculated according to an empiric relationship provided by BOTTRELL *et al.* (1976) as given in Eq. (4.15). Please note, that this empirical equation needs the temperature (T_C) to be given as degrees Celsius (and not as Kelvin as in the energy allocation model).

$$D = exp\big(bottrell.a + bottrell.b\ln(T_C) - bottrell.c(\ln(T_C))^2\big) \qquad (4.15)$$

The presented energy allocation rules fully specify individual growth and reproduction at a given constant food concentration. Individuals grow up to a food dependent maximal body size where somatic growth becomes zero. All parameters were derived from physiological measurements or direct observations (Table 4.1). Two additional parameters describing mortality rate and maximal lifespan of an individual will be introduced and discussed in the next sections.

4.3.2 The special case of starvation

Once food becomes a dynamic variable, situations may arise where energy intake does not meet energy demand and the individual suffers food shortage, that is net somatic growth rate becomes negative. Under such conditions individual body weight decreases whereas body length remains constant because *Daphnia* cannot shrink. Therefore, the approach in GURNEY *et al.* (1990) was adopted and an additional property, weight for length W_L, was introduced. The weight for length is that body weight that corresponds to the current body length according to the length-weight relationship given in Eq. (4.2). In the model system *Daphnia*, weight for length is an individual level property that can only change during molting. Consequently, starvation was defined as a situation where current weight W is below weight for length W_L.

Under starvation individuals sacrifice reproduction for somatic growth, i.e. they give priority to recover body weight (THRELKELD, 1987). In consequence, energy

allocation factor κ becomes one (Pseudocode with "$\leftarrow$" as assignment operator):

$$\text{if } (W < W_L) \quad \kappa \leftarrow 1 \tag{4.16}$$

Although is seems obvious that energy allocation should change under starvation in order to extend survival, an application of a step function is somewhat arbitrarily. One should rather expect a smoother physiological switch in this respect. Besides that, an application of a continuous function appears to be easier to handle in terms of the numerical integration of the ODE's and would have a dampening effect. However, empirical information about the physiological response to starvation in terms of resource allocation is limited and the step function was chosen for the sake of simplicity.

It has frequently been observed that *Daphnia* can suffer starvation for a distinct time without dying (ELENDT, 1989; ROHRLACK *et al.*, 1999a) but decrease in biomass. URABE & WATANABE (1990, 1991) measured length-weight relationships at different food concentrations and showed that body weight at very low food supply can be 50-70 % of the weight at rich food supply. However, if current weight falls below a distinct critical weight W_{crit}, starvation mortality d_s occurs that has to be added to background mortality rate d_b. The mortality rate d_s at conditions of strong starvation was set to $0.35\,\mathrm{d}^{-1}$ ROHRLACK *et al.* (1999b):

$$\text{if } (W < W_{crit}) \quad d \leftarrow d_b + d_s \tag{4.17}$$

According to URABE & WATANABE (1990, 1991) critical weight W_{crit} was assumed to be 60 % of the weight for length, thus, factor p_m was set to 0.6:

$$W_{crit} = W_L p_m \tag{4.18}$$

Application of this starvation concept produces mean starvation times of 4 days as observed in TESSIER *et al.* (1983).

4.3.3 Population level

Simulation of a *Daphnia* population was performed by means of a stage structured population model. The escalator boxcar train (EBT) framework, which was developed by DE ROOS *et al.* (1992), provides a sophisticated approach to this purpose and was used in this study to allow the application of the bioenergetic model on the

population level. Although a thorough description of this technique and an exemplary application to *Daphnia* is given in DE ROOS *et al.* (1992, Table 1D: food-dependent size-structured model with continuous reproduction), a summary of this concept is given in the appendix (see section 4.6) including relevant process rates of the EBT-framework and their assignments to the respective process rates of the underlying individual level model. An implementation of the EBT, which is written in **R**, is available from the author.

The basic principle of the EBT is to divide a population into a distinct number of cohorts each representing a defined age class of individuals (cohort width is typically one day). A cohort itself is characterized by its abundance and by individual level properties (e.g. body size, clutch size) representing mean values over all individuals within this cohort. In consequence, a cohort can be processed like an individual and the above-defined equations of the individual level model can be applied to describe the development of a cohort over time (e.g. increase in body size). After numerical integration of all relevant rates over one day a renumbering operation of all cohorts describes the shift in age structure within the population, a new cohort of neonates is added at the lower end of the boxcar train and the formerly oldest cohort is removed from the population, i.e. dies through ageing. The cohort in creation is continuously filled up with individuals through reproduction in between of two renumbering operations. Mean body size of individuals in this new cohort is calculated with a first order Taylor expansion term of somatic growth rate (see appendix 4.6).

Continuous dynamics of all cohorts are given in Table 4.2. The individual level model specifies physiological rates involved in the cohort dynamics, which directly accounts for ingestion rate (I) and somatic growth rate (g). Mortality rate (q) of the cohorts comprises of background mortality rate d_b and the starvation related mortality rate d_s that acts at conditions of strong starvation as indicated above. For the latter, an additional data structure has to be provided during the simulation in order to store current values of weight for length W_L of each cohort. Simulation of size-selective predation, i.e. when mortality rate becomes a function of body size, would require an additional first order Taylor expansion term for the simulation of abundance in the cohort in creation (compare DE ROOS *et al.*, 1992). Although a structure to include size-selective predation into the population dynamics simulation is completely implemented and available within the framework, this study assumes a constant mortality rate for the sake of simplicity.

Table 4.2: Escalator boxcar train (EBT) formulation for the individual level model

T	Temperature
F	Food concentration
D	Egg development time
N_i	Number of individuals in the ith cohort
W_i	Mean size of individuals in the ith cohort
E_i	Mean clutch size in the ith cohort
π_0	Total size mass, relative to W_b, of the individuals in the cohort in creation
W_b	Body size of a newborn
n	Number of cohorts (i.e. lifespan if box widths is one day as in this study)
$g(F,T,W_i)$	Somatic growth rate (depends on food concentration, temperature, and individual body size)
$q(F,T,W_i)$	Mortality rate (can be defined in dependence of food concentration, temperature, and individual body size)
$p_E(F,T,W_i)$	Reproductive rate expressed as produced eggs per time (depends on food concentration, temperature, and individual body size)
$I(F,T,W_i)$	Ingestion rate (depends on food concentration, temperature, and individual body size)
q_w, g_w	Derivatives of $q()$ and $g()$ in respect to body size W (approximation by first-order Taylor expansion)
$\mu_{F,max}$	Maximal growth rate of food algae
K	Carrying capacity of food algae
Dynamics of the cohort in creation (until first renumbering operation)	$\frac{dN_0}{dT} = -q(F,T,W_b)N_0 - q_w(F,T,W_b)\pi_0 + \sum_{i=1}^{n} = \frac{1}{D}E_iN_i$ $\frac{d\pi_0}{dT} = g(F,T,W_b)N_0 + g_w(F,T,W_b)\pi_0 - q(F,T,W_b)\pi_0$

— to be continued on next page . . . —

Table 4.2 continued from previous page

Dynamics of all cohorts in between two renumbering operations	$\frac{dN_i}{dT} = -q(F,T,W_i)N_i$ $\frac{dW_i}{dT} = g(F,T,W_i)$ $\frac{dE_i}{dT} = p_E(F,T,W_i) - \frac{1}{D}E_i$
Renumbering operation and initial values for the cohort with newborns (first cohort)	$N_1(t+\triangle^+) \leftarrow N_0(t+\triangle^-)$ $W_1(t+\triangle^+) \leftarrow W_b + \frac{\pi_0(t+\triangle^-)}{N_0(t+\triangle^-)}$ $N_0(t+\triangle^+) \leftarrow 0$ $\pi_0(t+\triangle^+) \leftarrow 0$
Renumbering operations for all other cohorts	$N_{i+1}(t+\triangle^+) \leftarrow N_i(t+\triangle^-)$ $W_{i+1}(t+\triangle^+) \leftarrow W_i(t+\triangle^-)$ $E_{i+1}(t+\triangle^+) \leftarrow E_i(t+\triangle^-)$
Dynamics of the food concentration	$\frac{dF}{dT} = F\mu_{F,max}\frac{K-F}{F} - \sum_{i=0}^{n} = I(F,T,W_i)N_i^*$

The presentation of the EBT follows DE ROOS *et al.* (1992). All included rates, e.g. somatic growth rate, reproductive rate, mortality rate, are declared in the individual level model including the assumptions about starvation. Parameter values are the same as for the individual level model (see Table 4.1); further explanations see text. Index *i* indicates the cohorts each of them representing an age group that was born within one day. Definition of cohorts might be different in other applications, e.g. individuals born within 12 h or 2 d. Body size is expressed as weight. At renumbering operations we used $(\leftarrow)$ as assignment operator and $(t+\triangle^-)$ and $(t+\triangle^+)$ denote state variables immediately before and after the renumbering operation, respectively. The quantity π_0 is a size measure in the cohort in creation and expresses the total size mass (i.e. the summed mass of all individuals) relative to size of neonates W_b. Technical aspects of the EBT-framework are further elaborated in the appendix (see section 4.6 on page 76).

* Include the zeroth cohort if $\lambda_0 \neq 0$.

Reproductive rate is expressed as eggs produced per individual per day and is calculated by dividing carbon investment into gonads by parameter c_E according to Eq. (4.14). In the original work of DE ROOS *et al.* (1992), reproductive rate is directly used to fill up the cohort in creation, i.e. produced eggs are converted immediately

into newborns. This arises from the necessity to model reproduction as a continuous process on the population level but deviates from *Daphnia* life history where eggs are stored in the brood chamber for one egg development cycle. Population models in general do not account for this characteristic time lag between egg production and release of neonates in *Daphnia*. To overcome this shortcoming the EBT framework was extended and a new cohort property have been introduced: the clutch compartment E_i. This new compartment represents the eggs deposited into the brood chamber, i.e. clutch size. Reproductive rate refills the clutch compartment. Neonates are released from the clutch compartment with an egg release rate, which is the inverse of egg development time D as given in Eq. 4.15 (calculated according to BOTTRELL *et al.*, 1976).

Food dynamics in the population model were modelled as in DE ROOS *et al.* (1992). Algal growth was simulated as logistic growth with a maximal growth rate $\mu_{F,max}$ and a carrying capacity K.

4.4 Results and discussion

4.4.1 Individual level

Somatic growth of individuals follows von Bertalanffy growth (Eq. 4.19) that is body length L can be calculated directly as a function of age (t). Both parameters of the von Bertalanffy equation, maximal body length L_{max} and von Bertalanffy growth coefficient k can be computed from the model parameters according to Eqs. (4.20) and (4.21). Body length at age = 0 (L_0) corresponds to the size of neonates and W_0 refers to the weight of neonates ($W_0 = a * L_0^3$).

$$L(t) = L_{max} - (L_{max} - L_0)e^{-kt} \tag{4.19}$$

$$L_{max} = \frac{\kappa f(F) p_{ing}\big(E_{A,max} - (E_{A,max} - E_{A,min}) f(F)\big)}{m_{F,min} + (m_{F,max} - m_{F,min}) f(F)} a^{-\frac{1}{3}} \tag{4.20}$$

$$k = \frac{\kappa f(F) p_{ing}\big(E_{A,max} - (E_{A,max} - E_{A,min}) f(F)\big) W_0^{\frac{2}{3}} - W_0\big(m_{F,min} + (m_{F,max} - m_{F,min}) f(F)\big)}{3aL_0^2(L_{max} - L_0)\big(f(T)\big)^{-1}} \tag{4.21}$$

Maximal body size (in μg C) is a function of food concentration. It increases asymptotically towards an absolute maximum of roughly 25 μg C. Note that this body weight is a measure of somatic biomass only, and that total carbon content of large adults can be substantially higher owing to carbon present within gonads or in eggs/embryos in the brood chamber that may make up to 40 % of the total body carbon (BOERSMA & VIJVERBERG, 1994a). The predicted maximal weight corresponds to a body length of 2.6 mm (FLÖSSNER, 2000). The model considers no effect of temperature on maximal body size. This arises from the assumption that ingestion and maintenance rate are both affected by an identical Arrhenius scale as stated in DEB theory (KOOIJMAN, 2001). Nevertheless, several authors described a decrease in maximal body size with increasing temperature for zooplankters (MCLAREN, 1963; HALL, 1964; MOORE *et al.*, 1996) and it is generally assumed that this phenomenon originates from faster increasing catabolic rates than anabolic rates with rising temperature (MOORE & FOLT, 1993; WEETMAN & ATKINSON, 2004). Evidently, there is a strong need for more information about temperature dependence of physiological rates to solve this problem satisfactorily.

Temperature markedly influences the shape of somatic growth curves reflecting the temperature dependence of the von Bertalanffy growth coefficient k: The lower ambient temperature the slower somatic growth (Fig. 4.2). This pattern, which was proven by several experimentalists (HALL, 1964; VIJVERBERG, 1980; GOSS & BUNTING, 1983) and model studies (e.g. RINKE & PETZOLDT, 2003), is also responsible for an increase in age at maturity with decreasing temperature (Fig. 4.3). Food limitation can as well induce delayed maturation owing to slow somatic growth (Fig. 4.3). Observations of age at maturity at different temperatures and food concentrations closely resembled these predicted patterns (LYNCH, 1992; GIEBELHAUSEN & LAMPERT, 2001).

Size at first reproduction (SFR) increases asymptotically with food concentration (Fig. 4.4). Differences in SFR are due to differences in length increase when the first adult instar molts into the second adult instar. Length increase within this instar depends on food concentration leading to different SFR at different food concentrations although SAM is a constant. Life-table studies of *Daphnia* have often shown this asymptotical increase of SFR with food concentration (MCCAULEY *et al.*, 1990a; BOERSMA & VIJVERBERG, 1994a, 1995b; GIEBELHAUSEN & LAMPERT, 2001) and this model provides for the first time a mechanistic explanation for this observation.

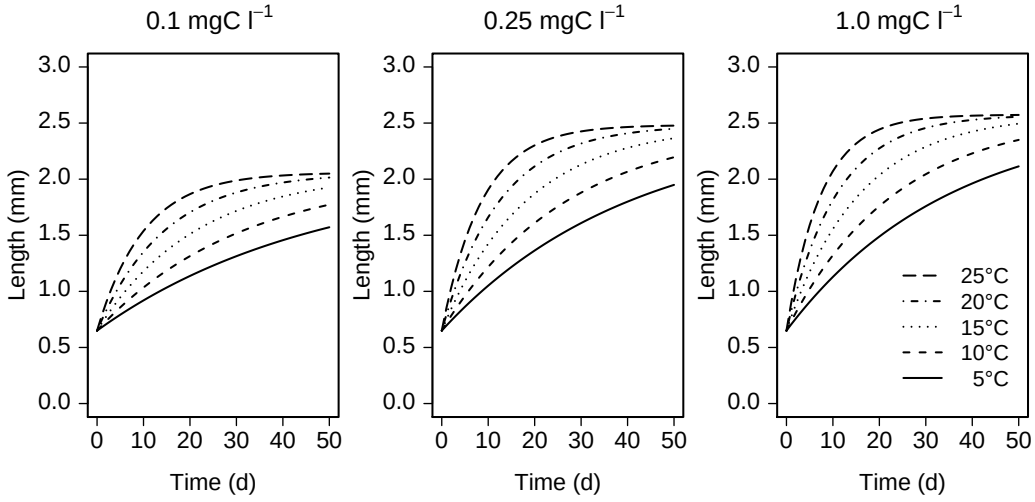

Figure 4.2: Predicted somatic growth of *Daphnia galeata* at different food concentrations and temperatures. Food concentration is given at the top of each panel.

Besides food-dependence, variability in *SFR* is further influenced by several other factors like predator kairomones (MACHÁČEK, 1991; STIBOR, 1992), maternal effects (LAMPERT, 1993b), and clone-dependent differences (DE MEESTER & WEIDER, 1999). However, such factors can be easily incorporated into our model. For instance, the effect of predator kairomones on daphnid life-history can be simulated by changing SAM and the energy allocation factor κ (see next chapter, ch. 5, and compare STIBOR & LÜNING, 1994).

Comparison of model outputs with the observations from the life-table experi-

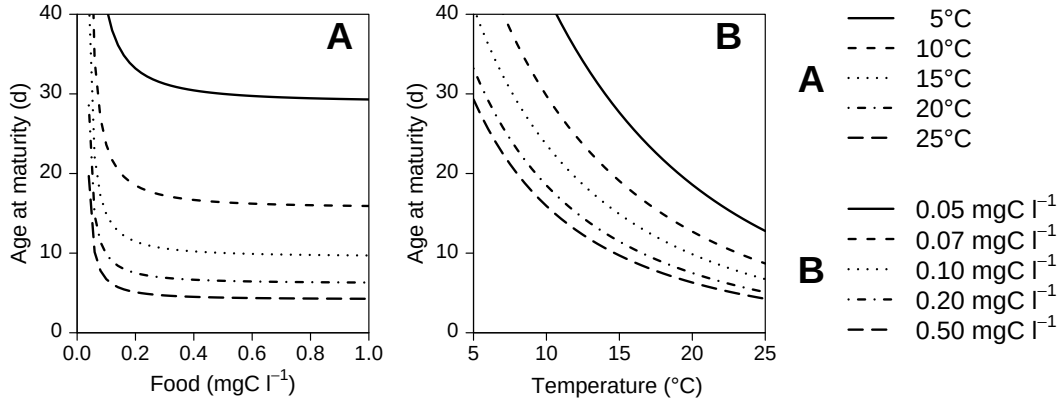

Figure 4.3: Age at maturity of an individual *Daphnia galeata* in relation to food concentration (A) and temperature (B).

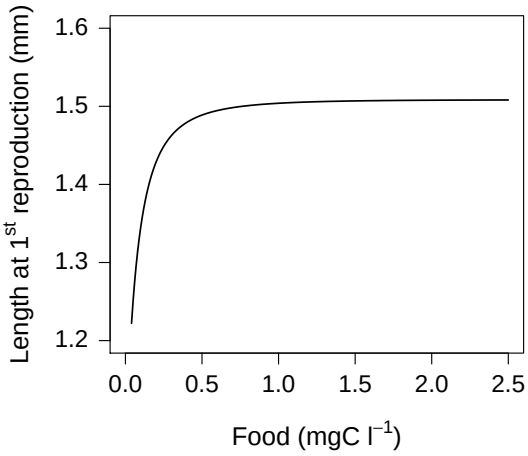

Figure 4.4: Body length at first reproduction (i.e. first occurrence of eggs in the brood chamber) as a function of food concentration.

ment showed an excellent agreement (Fig. 4.5). Besides somatic growth and length-dependent egg production, the model is also able to reproduce age-dependent egg production, which is the most critical criterion because both processes – somatic growth and egg production – come here into play. All parameter values applied to this model run were used as stated above, i.e. no parameter fitting was used for parameter estimation. Hence, the agreement between life-tables and model outputs represents an independent validation of the model. The threshold food concentration for egg production predicted by the model is about 0.04 mg C L^{-1} and close to the observed food thresholds for *D. galeata* in life-history experiments (GLIWICZ, 1990; KREUTZER & LAMPERT, 1999). For the fist time, known so far to the author, an individual level model of *Daphnia* has been validated to such an extremely low food concentration. Other approaches did not address food concentrations close to minimal food requirements (e.g. PALOHEIMO *et al.*, 1982; KOOIJMAN & METZ, 1984; GURNEY *et al.*, 1990) and, indeed, application of these models revealed problems due to deviating model behavior at low food concentrations (DE ROOS *et al.*, 1997).

In contrast to original DEB-theory, this approach did not include a reserve compartment as an additional individual level state variable due to limited empirical information about the energy flow from the reserve compartment into growth, maintenance and reproduction (see TESSIER & GOULDEN, 1982; TESSIER *et al.*, 1983). Nevertheless, it should be noted that under conditions of constant resource availability, omission of the reserve compartment led to the same model outcomes because

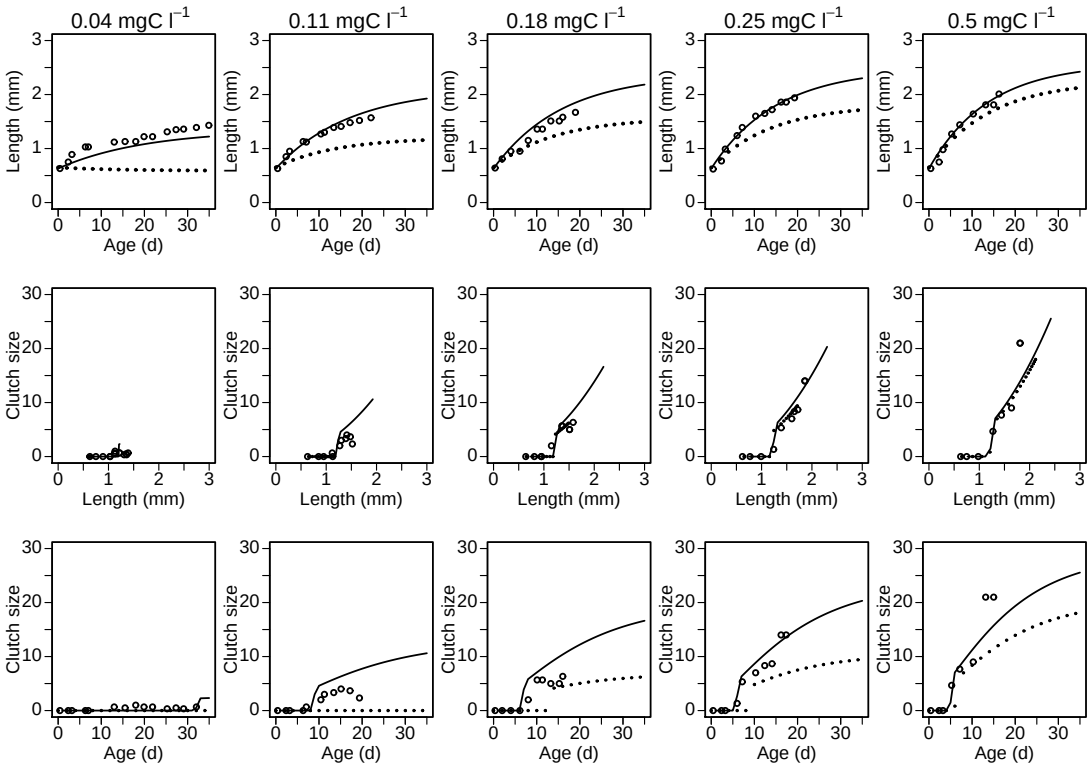

Figure 4.5: Model validation (solid line) on life-history data (open circles) of *Daphnia galeata* at different food concentrations as indicated at the top of each column. Model outputs are further compared to the Kooijman-Metz model (KOOIJMAN & METZ, 1984) of *Daphnia* (dotted line) as used in DE ROOS *et al.* (1992). Parameterization of the Kooijman-Metz model was adapted to *Daphnia galeata*. The upper panel denotes somatic growth as body length against age and the following rows shows clutch size as function of body length and as time series, respectively. Data of the life-table experiment were kindly provided by J. Vijverberg (NIOO-KNAW, Netherlands Institute of Ecology, Centre for Limnology, Nieuwersluis).

reserves would be in steady state. Under conditions of dynamic food supply or starvation, however, differences in model outcomes do occur. Whereas DEB-theory predicts depletion of reserves under starvation, our approach assumes a decrease of somatic biomass, i.e. decreasing body weight while keeping the same body length. This assumption leads to a variable length-weight relationship at conditions of variable food supply. Thus, the weight of an individual of a given length will differ according to the food conditions as was shown for both field and laboratory populations of *Daphnia* (BOERSMA & VIJVERBERG, 1994b).

Model outputs were further compared with corresponding predictions by the Kooijman-Metz model of *Daphnia* (KOOIJMAN & METZ, 1984) as used in DE ROOS *et al.*

(1992) at the five food concentrations applied in the life-history experiments (Fig. 4.5). In contrast to the approach presented in this study the Kooijman-Metz model assumes a constant assimilation efficiency and a fixed maintenance coefficient. At constant food concentration (i.e. steady state of reserves) these two aspects mark the difference between both model approaches. From this one can infer that at a given food concentration a parameterization of the Kooijman-Metz model exists that exactly matches those outputs calculated by the approach used in this study. Accordingly, the Kooijman-Metz model was parameterized in such a way that outputs of both models are identical at a food concentration of 1 mg C L^{-1}, which corresponds to an assimilation efficiency of app. 56 % and a maintenance coefficient of 0.23 d^{-1}. However, with this parameterization the Kooijman-Metz model failed to predict growth and reproduction at food conditions below 0.15 mg C L^{-1} (Fig. 4.5). Of course, the reference food concentration used for model parameterization (i.e. 1 mg C L^{-1}) was chosen arbitrarily and one can easily parameterize the Kooijman-Metz model in order to fit growth and reproduction at such low food concentrations. But, however, then individual development at higher food concentrations would deviate from observations, i.e. would be overestimated. Individual *Daphnia* optimize energy acquisition and maintenance requirements at low food concentrations and the Kooijman-Metz model lacks the structure to account for this. Thus, adaptations to low food conditions in terms of assimilation efficiency (increased) and maintenance coefficient (reduced) appeared to be an important feature of daphnid performance at such food concentrations and has to be included in bioenergetic models of *Daphnia* (PORTER *et al.*, 1982; BOHRER & LAMPERT, 1988; URABE & WATANABE, 1990, 1991).

4.4.2 Population level

Simulations of the structured population model showed large cycles of *Daphnia* abundance and its algal prey (Fig 4.6, upper panel). Rapidly increasing *Daphnia* population size at high food concentration was immediately followed by a sharp decline of algal biomass. Remarkably, daphnid abundance proceeded to increase for a few days when algal biomass had already collapsed. This overshooting of *Daphnia* abundance is due to further release of neonates from eggs within the brood chamber of adult individuals. Reproduction, i.e. production of eggs, already ceased during this period owing to food limitation. Individuals even suffered starvation as could be seen in decreasing population biomass. Both, high food demand of the surviving population and

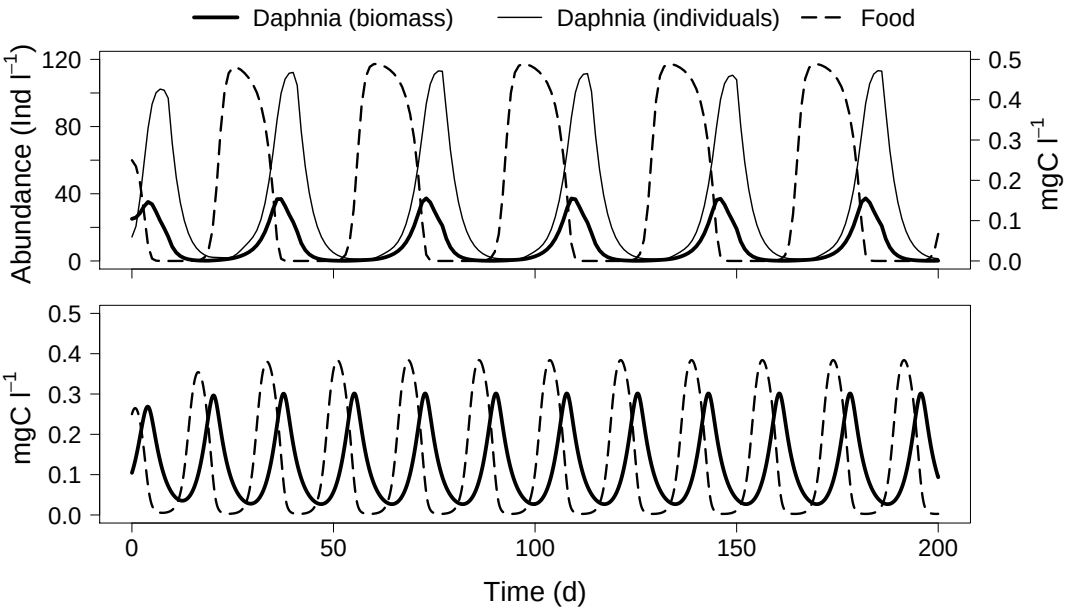

Figure 4.6: Dynamics of a *Daphnia galeata* population simulated by the structured population model (upper panel) in comparison to a simulation using a classical unstructured population model (lower panel). Solid lines represent *Daphnia* biomass (bold line) and individual abundance (thin line); the dashed line shows algal dynamics. Temperature was set to 17.5°C. Model specification of the unstructured model is provided in Table 4.3.

delayed reproductive output by adult individuals led to a tremendous overexploitation of resources by *Daphnia*. Finally, the breakdown of algal biomass was followed by a collapse of *Daphnia* itself, which was induced by non-consumptive mortality like starvation and ageing. Once the *Daphnia* population has collapsed, algae recover with high growth rates and even approach their carrying capacity before a new cycle of *Daphnia* starts (prey escape cycles).

Cycles of daphnid and algal abundance were characterized by a relatively long cycle interval leading to pronounced clear water phases with low algal biomass (Fig. 4.6). Duration of this clear water phase was almost three weeks. The first half of the clear water phase was associated with high *Daphnia* abundance, a phenomenon frequently observed in the field (LAMPERT *et al.*, 1986; HÜLSMANN, 2003). The clear water phase was dominated by individuals that were almost entirely born during the end of the exponential growth phase (Fig. 4.7), i.e. population dynamics of *Daphnia*

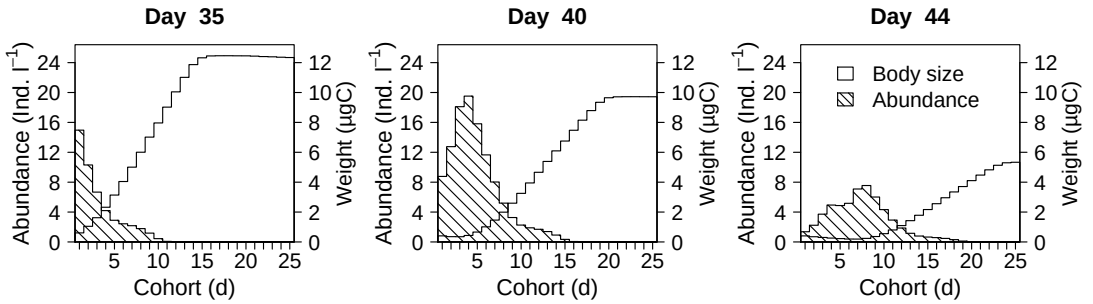

Figure 4.7: Age structure of the *Daphnia* population in the simulation presented in Figure 4.6 at different times. On day 35 (short before biomass peak) the population shows an age structure typical for exponential growth. Five days later (after biomass peak) the peak cohort becomes prominent. A population consisting almost only of small individuals due to starvation and non-consumptive mortality is present on day 44 (app. 10 days after initiation of the clear water phase).

displayed single generation cycles (MCCAULEY *et al.*, 1999).

Emerging patterns of population dynamics in the EBT-model simulation (Figs. 4.6 and 4.7) showed a typical sequence of consecutive events: exponential growth of *Daphnia* → formation of a peak cohort → overexploitation of resources → non-consumptive mortality during the clear water phase. Such patterns were likewise found in investigations of the midsummer decline of *Daphnia* in the hypertrophic Bautzen reservoir (HÜLSMANN & VOIGT, 2002; HÜLSMANN, 2003) as well as in mesocosm experiments (MCCAULEY *et al.*, 1999). In the field, typically only one such cycle is completed because after the decline daphnids are depressed by predation and shifts within the phytoplankton community towards inedible or toxic species (SOMMER *et al.*, 1986). It appeared to be a characteristic property of *Daphnia* population dynamics to overexploit their resources after a period of very intense reproduction. High growth rates and fluctuating demography thus can be interpreted as a precursor of a tremendous population breakdown. In this respect it is noteworthy that maximal population growth rates in our simulation were almost twice as high as maximal population growth rates under steady state conditions (about $0.3\,\mathrm{d}^{-1}$), i.e. with a stable age distribution. In an analysis of long-term data of the biomanipulated Bautzen reservoir, BENNDORF *et al.* (2001) found comparable patterns of *Daphnia* population dynamics. They argued that in years with slowly increasing *Daphnia* populations the following clear water phase was relatively short and a catastrophic breakdown of the population was unlikely. Possible dampening factors during population growth might

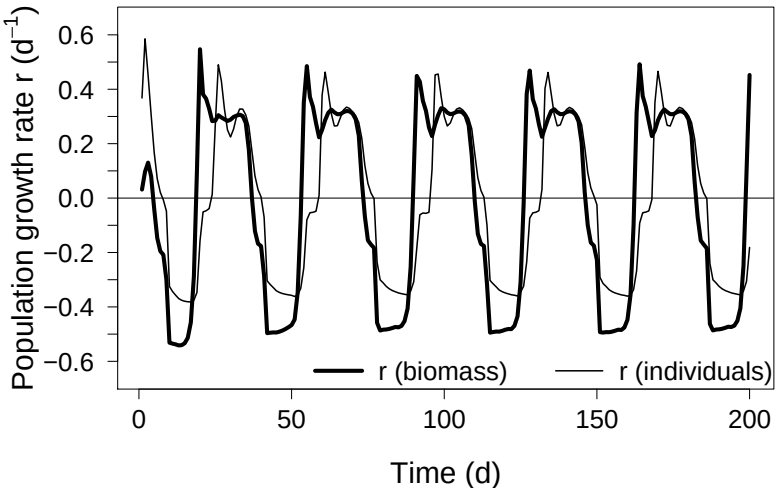

Figure 4.8: Population growth rate *r* computed from the model run of the structured population model (see Fig. 4.6, upper panel). Rates were calculated from either individual abundance (thin line) or from total population biomass (bold line).

be lowered temperature, poorly ingestible algae, predation or production of resting eggs (GLIWICZ & LAMPERT, 1990; MCCAULEY *et al.*, 1999; BENNDORF *et al.*, 2001).

In contrast to unstructured population models this new approach provided information about: (1) population abundance and (2) population biomass. Contrary to expectations, these two properties did not correlate; differences appeared in population rate of increase r calculated from either abundance or biomass (Fig 4.8). These emerging differences in population rate of increase were caused by demographic effects, starvation and delayed reproduction. Extreme events in this respect are populations suffering initiatory starvation, which decrease in biomass but still increase in abundance, or populations that recover from starvation (vice versa). By plotting pairs of population rate of increase against food concentration (Fig 4.9) the complex interaction of demography and physiological state with population growth rate, respectively, became even more prominent. At a distinct food concentration different growth rates have been realized. The relationship between population growth rate and food concentration is variable and different from those applied in classical population models that normally assume a hyperbolic function (Fig 4.9; dashed line).

Considering the logic of unstructured population models, which assume a fixed relationship between resource availability and population growth rate, it explicitly emerges that both approaches should predict different dynamics (Figs. 4.9). In order

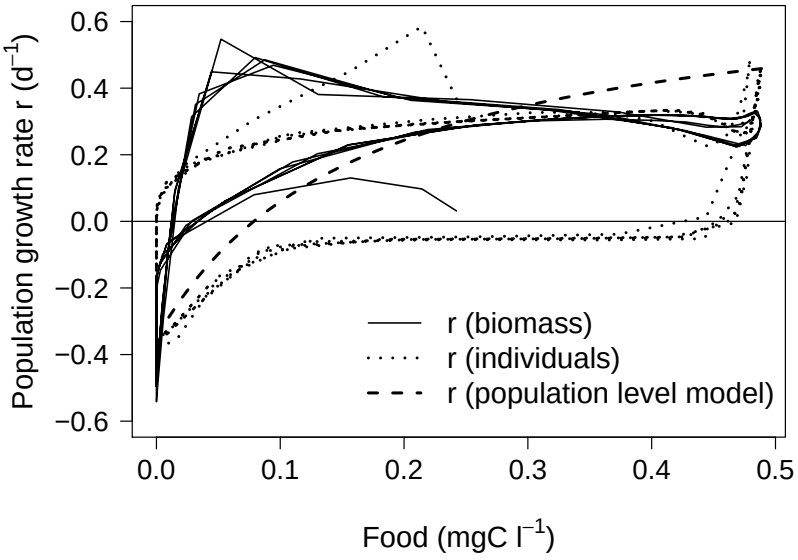

Figure 4.9: State diagram of population growth rate *r* derived from the model run of the structured population model (see Fig. 4.6, upper panel) plotted against corresponding food concentration. Rates were calculated from either individual abundance (dotted line) or from total population biomass (solid line). A time series of 200 days was used for the plot. The dashed line indicates the food-dependent population growth rate *r* for a classical unstructured population level model as specified in Table 4.3 and applied in Fig. 4.6 (lower panel).

to investigate the differences between both population level approaches even further, simulations of the structured population model were compared with simulations of an unstructured population model (Fig. 4.6, lower panel). Specification of the unstructured population model is given in Table 4.3 and resource-dependent population growth rates correspond to the population model depicted in Fig. 4.9 (dashed line). Simulations with the unstructured population model showed typical predator-prey cycles. Relative differences between minima and maxima were less pronounced than in the EBT-model. Cycle length of *Daphnia*-biomass was about 17 days in the unstructured population model and markedly reduced in comparison to the structured model (36 days). Algal dynamics were dampened in the unstructured model and displayed neither prominent overexploitation by *Daphnia* nor prey-escape cycles. No prominent clear water phase was visible in the unstructured population model.

Existing models of *Daphnia* that allow variable food and temperature conditions mostly belong to the type of classical, i.e. unstructured, population models. A detailed study of temperature effects on phytoplankton-zooplankton interactions was presented

Table 4.3: Model specification of the unstructured population model (Fig. 4.9, dashed line). X: algae (mg C L^{-1}); Z: zooplankton (mg C L^{-1}).

$$\frac{dX}{dt} = X\mu_{max}\frac{K_A - X}{K_A} - ingestion\,Z$$
$$\frac{dZ}{dt} = ingestion\,e_A Z - (r_Z Z + m_Z Z)$$
$$ingestion = i_Z Z\frac{F}{k_{ing} + F}$$

with:

Parameter	Description	Value	Unit
μ_{max}	maximal growth rate of algae	1.2	d^{-1}
K_A	carrying capacity of algae	0.5	mg C L^{-1}
i_Z	specific ingestion rate of zooplankton	1.8	dimensionless
k_{ing}	half saturation constant for ingestion	0.164	mg C L^{-1}
e_A	assimilation efficiency	0.6	dimensionless
r_Z	respiration rate of zooplankton	0.3	d^{-1}
m_Z	mortality rate of zooplankton	0.05	d^{-1}

by NORBERG & DEANGELIS (1997), who also used an unstructured model. They calculated equilibrium points for the model states and the stability of these equilibria by means of Eigenvalues. Such techniques represent powerful tools for the analytical investigation of population models. Although DE ROOS (1997) also developed techniques for the analytical evaluation of EBT-models, the application of such techniques is rather complicated and in some respects still limited (e.g. bifurcation analysis). However, from the empirical perspective it is sometimes hard to judge, which results of such analytical evaluations of simplified models are relevant for the real system. Moreover, planktonic systems in particular are believed to be seldom in an equilibrium state (HUTCHINSON, 1961; SCHEFFER *et al.*, 2003). Although NORBERG & DEANGELIS (1997) presented references for the empirical evidence of all parameters used in their model, they did not compare their model outputs with relevant observations, i.e. no model validation was carried out, which curtails interpretation of model results for empirical scientists. So, one might loose mathematical manageability when switching from unstructured to structured population models but – at least for the example of *Daphnia* – one will gain on the other hand a mechanistically based model

structure that is more akin to the real system and successfully reproduces such patterns observed in the laboratory and in the field.

In comparison to the original EBT-model by DE ROOS *et al.* (1992) the approach presented here includes two new aspects: (i) the inclusion of a variable temperature and (ii) the introduction of the clutch compartment, which allows to take the cladoceran life cycle into account, i.e. the time lag between the release of eggs into the brood chamber and the release of neonates out of the brood chamber. This delay in reproduction was implemented earlier by NISBET *et al.* (1989) and MCCAULEY *et al.* (1996) in structured population models of *Daphnia* by using delay-differential equations but these models were developed under the assumption of a constant temperature. Of course, the most adequate model structure to account for special life cycle characteristics of *Daphnia* would be an individual based model (MOOIJ & BOERSMA, 1996, and compare the model approach presented in chapter 3). A recently presented, further developed version of the model of MOOIJ & BOERSMA (1996) was even successfully applied to the simulation of field populations (MOOIJ *et al.*, 2003). However, for this purpose a standard egg production, which is interpreted as a measure of food availability, is needed as driving factor. Thus, food concentration is not included as a state variable as in this study but has to be given as a function of time. Among existing individual level models of *Daphnia* that are based on energy allocation only a few incorporated variable temperature (WULFF, 1980; KOH *et al.*, 1997). KOH *et al.* (1997) even used their model for a population model by using a partial differential equation approach. However, thorough validation of model outputs as shown in the present study is lacking in their paper, which, again, hampers any further interpretation. The model framework presented here overcomes the constraints discussed above and might be a promising tool for the simulation of *Daphnia* populations even under natural conditions, e.g. in population dynamics studies or as submodel integrated within ecosystem models.

4.5 Conclusions

The presented model framework provides a general tool for the simulation of individual and population level dynamics of *Daphnia* under varying temperature and food concentration. Two levels of biological organization (individual - population) are included and allow a broad spectrum of possible applications; be it on the individual

(e.g. life-history theory), on the population (population dynamics), or even on the ecosystem level (food web studies). Special physiological adaptations of individual *Daphnia* in terms of energy acquisition and energy usage have been included that appeared to be important features of growth and reproduction at very low food concentrations. Data from a life-table experiment were used for model validation and proved that model outputs are consistent with the observations. Model structure is open for inclusion of further processes and state variables (e.g. poorly ingestible algae).

It was further shown, that population dynamics of *Daphnia* displayed by the structured population model correspond very well with the patterns observed in the field (e.g. HÜLSMANN, 2003). In contrast to this, classical unstructured population models were found to be a less suitable approach to the simulation of *Daphnia* populations under field conditions owing to their inability to incorporate demographic effects and associated processes. Difficulties in simulating zooplankton with classical population models have been recognized by some model studies on the ecosystem scale (e.g. BENNDORF & HORN, 1985; HAMILTON & SCHLADOW, 1997; OMLIN *et al.*, 2001). Altogether it is strongly suggested that unstructured models are not appropriate for the simulation of organisms displaying a rapidly changing demography. Aggregation errors emerging from the transition of a demographically structured population into a unified average population can be of considerable influence. Therefore, structured population models might be a promising approach to increase our abilities to perform a more realistic simulation of organisms with highly dynamic demography like *Daphnia*. This might be especially appropriate for the zooplankton compartment within lake models.

4.6 Appendix

The basis of the EBT-framework is to divide a population into distinct cohorts and describe their development over time continuously by ODEs and the renumbering of these cohorts in equidistant time intervals. Each cohort is characterized by the following states: individual weight W, clutch size E, and abundance N. Individual weight W of cohort i changes over time according to Eq. 4.22. Relevant processes are assimilation rate (A) and maintenance rate (M) that are specified by Eqs. 4.5 and 4.7 – 4.13 of the individual level model and by equation 4.16 for the special case of starvation.

$$\frac{dW_i}{dt} = \kappa_i A_i(F,T) - M_i(F,T) \tag{4.22}$$

Individual clutch size E of cohort i changes over time through production of new eggs and the release of newborns (Eq. 4.23). Egg production is described by Eqs. 4.6 – 4.11 and Eqs. 4.14 – 4.16 of the individual level model. Note that, according to the individual level model, only cohorts that are mature can produce eggs (see Eq. 4.23). Mature cohorts are defined by a weight W_i above weight at maturity (WAM, calculated from SAM according to Eq. 4.2). Release of newborns is a first order loss term of clutch size E proportional to the inverse of egg development time D.

$$\frac{dE_i}{dt} = \begin{cases} 0 & \text{if } W_i < WAM, \\ \left(\dfrac{(1-\kappa_i)A_i}{c_E} - \dfrac{1}{D}\right)E_i & \text{if } W_i > WAM. \end{cases} \tag{4.23}$$

Abundance of cohort i is only influenced by mortality, which is a first order loss term (Eq. 4.24). There is no gain term for the cohorts because all newborns were directly released into the cohort in creation (see below). Mortality rate $q_i()$ of cohorts is defined by background mortality rate d_b and starvation-related mortality d_s as described by Eqs. 4.17 – 4.18, i.e. cohorts suffering strong starvation ($W_i < W_{i,crit}$) are, besides background mortality d_b, also affected by starvation induced mortality d_s. Note that for this calculation the current weight for length of the respective cohort ($W_{L,i}$) has to be provided by an appropriate data structure. In the model structure $W_{L,i}$

is incorporated as a property of each cohort.

$$\frac{dN_i}{dt} = -q_i()N_i \tag{4.24}$$

The cohort in creation acts as a pool collecting all newborns released by the population within one day. Abundance of this cohort increases by summed reproductive rate over all cohorts and deceases by mortality rate as defined above (see Table 4.2). If one might formulate mortality rate as a direct function of body size W (e.g. size selective predation) an additional term q_w, which represents the first order-Taylor expansion of $q(W)$, has to be included as indicated in Table 4.2. However, in order to keep the model simple a mortality rate independent of body size have been used in the simulations, thus q_w equals zero.

Body size W_0 of the cohort in creation is hard to describe in a direct way because the value of W_0 and its dynamics are undefined at the time that the cohort is started, i.e. when it is empty. To overcome this difficulty, individual body weight of the cohort in creation is described as total size mass π_0. This measure is defined as the total biomass of individuals in the cohort in creation at time t relative to the size at birth W_b (Eq. 4.25 and compare Table 4.2).

$$\pi_0(t) = (W_0(t) - W_b)\,N_0(t) \tag{4.25}$$

Since somatic growth rate changes with body weight, an additional Taylor expansion term g_w of somatic growth rate has to be included as indicated in Table 4.2.

During the simulation ODEs of all cohorts (including the cohort in creation) given above were integrated over one day (internal integration time step was 0.05 d), i.e. over the period equal to the width of the age classes. Then renumbering of all cohorts is carried out by removing the oldest cohort, incrementing the cohort number i of the remaining cohorts, and transferring the cohort in creation into the first cohort ($i = 1$). According to Eq. 4.25, body weight of the first cohort W_1 is calculated by adding W_b to total size mass of the cohort in creation divided by its abundance (Eq. 4.26).

$$W_1 = W_b + \frac{\pi_0}{N_0} \tag{4.26}$$

5 Adaptive value, energetic costs, and underlying resource allocation patterns of predator-induced life-history shifts in *Daphnia*[1]

Abstract

This chapter focuses on costs and benefits of life history shifts of water fleas (genus *Daphnia*) in response to infochemicals from planktivorous fish. For this purpose, a thoroughly validated dynamic energy budget model is applied to investigate the resource allocation patterns underlying the observed life history shifts and their adaptive value under size selective predation in one coherent analysis. Using a published data set of life history shifts in response to fish infochemicals (DE MEESTER & WEIDER, 1999) it is shown that *Daphnia* invests less energy in somatic growth in the fish treatment. This observation complies with theoretical predictions on optimal resource allocation. However, the observed patterns of phenotypic plasticity cannot be explained by changes in resource allocation alone. The analysis of the empirical data with the dynamic energy budget model clearly showed additional energetic costs in the fish treatments. These costs give an explanation why the observed defences are inducible: the response to fish kairomones only becomes adaptive if the intensity of size selective predation surpasses a certain critical level. As far as known to the author, this is the first study that puts resource allocation, energetic costs and adaptive value of predator induced life-history shifts - using empirical data - into one theoretical framework.

[1] Main results of this chapter are going to be published in RINKE, K., S. HÜLSMANN & W.M. MOOIJ (submitted)

5.1 Introduction

A central paradigm of life history theory is that organisms allocate resources such that fitness, which is usually measured as the intrinsic rate of natural increase *r*, is optimized (STEARNS & KOELLA, 1986; STEARNS, 1992). Especially organisms with indeterminate growth, like *Daphnia*, constantly face a trade-off in the allocation of resources between growth and reproduction. This 'dilemma of energy allocation' stimulated a number of theoretical approaches on the evolution of life-histories, which is viewed as being an optimization process for resource allocation (e.g. GADGIL & BOSSERT, 1970; KOZLOWSKI, 1992; HEINO & KAITALA, 1999; SHERTZER & ELLNER, 2002). Indeterminate growth, i.e. growth that continues past maturation, is not easy to explain from an evolutionary perspective (HEINO & KAITALA, 1999); still it is characteristic for many invertebrate taxa like clams, cladocerans and crayfish, 'lower' vertebrate taxa like fish and amphibians and many plants. In all these organisms the fact that fecundity usually increases with body size constitutes a further trade-off between current and future reproduction. Additionally, other fitness-related factors like starvation resistance and survival probability depend on size (PETERS, 1983). In particular, predators feeding preferentially on specific size classes of their prey, e.g. planktivorous fish preying selectively on large zooplankton (LAZZARO, 1987), render survival probability of the prey to be strongly size-dependent.

Theoretical approaches to elucidate optimal resource allocation predict that in environments with reduced adult survivorship selection should favor earlier reproduction and increased reproductive effort, i.e. resource allocation into reproduction should be increased on the expense of somatic growth (REZNICK *et al.*, 2004). In environments with reduced juvenile survival selection should favor an opposite strategy (LAW, 1979). Studies on optimal resource allocation in the cladoceran *Daphnia* have been based on the partitioning of net production between somatic growth and reproduction (GABRIEL, 1982; TAYLOR & GABRIEL, 1992, 1993). They revealed an "on-off" strategy being most adaptive under conditions of positive size-selective predation as typically exerted by visually feeding fish (TAYLOR & GABRIEL, 1992). This means neonates consequently give 100 % of resources available towards somatic growth and as soon as size at maturity is attained resource allocation is immediately switched to entire allocation into reproduction. Such a strategy leads to determinate growth and individuals do not grow once they became adult, which runs counter to empirical results (LYNCH, 1980). Although *Daphnia* were proven to adapt its life-

history to size-dependent mortality regimes, there never occurs a switch from indeterminate to determinate growth. Adding seasonality to the model, TAYLOR & GABRIEL (1993) found at least slight adult somatic growth under positive size-selective predation. However, quantitative values of maximum adult size of *D. pulex* as predicted by their model still seem unreasonably low compared to empirical data (HANSEN & WAHL, 1981; WEIDER & PIJANOWSKA, 1993).

More importantly, underlying assumptions of their approach do not comply with empirical and theoretical knowledge about resource allocation in *Daphnia* and other organisms (see below). On the whole, for a proper understanding of life-history evolution in organisms with indeterminate growth it is not convincing to apply a model predicting determinate growth. This study, therefore, focuses on a new approach to link resource allocation with life-history by focusing exclusively on observed life-history shifts and explicitly accounting for the physiological properties associated with indeterminate growth, which circumvents the problematic assumptions of former studies. By applying this more realistic model to observed life-histories of *Daphnia*, it becomes feasible to study the underlying physiological mechanisms, the trade-offs and costs involved herein, and their evolutionary significance.

In comparison to further model approaches, the bioenergetic model used in this study exhibits three characteristics that account for the metabolic organization of organisms with indeterminate growth like *Daphnia*. Firstly, allocation into reproduction starts already early in the juvenile stage (ZAFFAGNINI, 1987; EBERT, 1992) and not only in the instar preceding the deposition of the first clutch as assumed in Taylor's studies. To reach maturity, a certain amount of energy is needed for the development of the reproductive machinery and its regulation systems; thus, overall costs of reproduction appeared to be higher than plain costs for egg production and they already account in juveniles (maturation costs, KOOIJMAN, 2001). Secondly, general patterns in resource allocation should be viewed as the result of an organisms metabolic organization that in many species showing indeterminate growth does not fundamentally change during life. For example, in 'Dynamic Energy Budget' models of *Daphnia* (DEB-models, KOOIJMAN & METZ, 1984; KOOIJMAN, 2000) the proportion of assimilated resources directed towards reproduction is described by a constant (the κ-rule, see KOOIJMAN, 2000; RINKE & VIJVERBERG, 2005). Moreover, for *Daphnia* it was shown that principal energy allocation patterns are fixed in the first 24h of life and afterwards do not fundamentally change (MIKULSKI *et al.*, 2004). To summarize

these both arguments, there is no physiological switch that conceptually corresponds to Taylor's "on-off" strategy. Thirdly, partitioning of net production, as done in Taylor's studies, implies neglecting any effects of maintenance on individual life-history. However, we have empirical evidence that maintenance costs dramatically change with body size and that maintenance costs are involved in shaping somatic growth (e.g. VON BERTALANFFY, 1957; WEST *et al.*, 2001). Consequently, this study uses a model that allocates gross production and explicitly takes maintenance costs into account.

Life histories and their underlying resource allocation patterns may vary between populations due to genetic differences (REZNICK, 1982; REZNICK *et al.*, 1990) or within a population as a result of clonal succession (PACE *et al.*, 1984) or simply due to phenotypic plasticity (e.g. RIESSEN, 1999; TOLLRIAN & HARVELL, 1999). Also for *Daphnia* it was suggested that selection should favor phenotypic variation in resource allocation if the animals can detect the type of predator (TAYLOR & GABRIEL, 1993), which indeed turned out to be the case: daphnids of the same clonal lineage differentially respond to chemical cues released by predators which prefer different size classes as prey (RIESSEN, 1999). When daphnids were exposed to water previously inhabited by fish (which select large individuals) reproductive effort (percentage of net production allocated into reproduction) was increased while somatic growth and size at maturity were reduced. When they sense invertebrate predators like *Chaoborus* (which selects small individuals) reproductive effort was reduced while somatic growth and size at maturity were increased (STIBOR, 1992; STIBOR & LÜNING, 1994; STIBOR & MACHACHEK, 1998). Nevertheless, most studies on predator-induced life history shifts did not measure reproductive effort which can easily be related to resource allocation patterns (this study), but rather focused on phenomenological characteristics like size and age at maturity, clutch size and neonate size (e.g. MACHÁČEK, 1991; BOERSMA *et al.*, 1998; DE MEESTER & WEIDER, 1999; SPAAK *et al.*, 2000; HÜLSMANN *et al.*, 2004). Focusing on predator-induced responses in these life history traits may, however, detract from the fact that these traits are only manifestations of the underlying resource allocation pattern and thus provide only minor information about the involved trade-offs. Indeed, this study suggests that predator kairomones induce a shift in an individuals general energy allocation scheme and that in the case of fish kairomones energy allocation to reproduction is increased, resulting in slower somatic growth and a reduced size at maturity as well as an increased re-

productive effort. Concerning clutch size and neonate size it must additionally be taken into account that these traits are themselves size-dependent. Consequently, they may not be directly compared between treatments where daphnids had been exposed to kairomones or not. Rather, their relations with body size may be compared (MACHÁČEK, 1991; HÜLSMANN *et al.*, 2004). Finally, such a shift in energy allocation may be associated with costs on the bioenergetic level, which are now going to become quantifiable by the model application.

The aim of this study is to investigate the underlying resource allocation patterns that are responsible for observed life-history shifts of *Daphnia* in response to fish predation. In contrast to earlier studies (GABRIEL, 1982; TAYLOR & GABRIEL, 1992, 1993) it is not intended to find an optimal resource allocation under a given predation regime, i.e. to design an optimal, but imaginary, life-history. Instead, empirical observations of life-history shifts in several clones of *Daphnia galeata* $\times$ *hyalina* are used to evaluate the resource allocation patterns behind these observations by means of a mechanistical model of resource allocation. In a second step, it is asked if and how far the observed life history responses to fish can be considered as being adaptive. To this end, the observed life-histories were used to calculate intrinsic rates of population growth under a broad range of predation regimes that are potentially exerted by visually hunting planktivorous fish. On the whole, this approach proposes a framework to bridge from physiological patterns in resource allocation over individual life-history and its plasticity towards adaptive value and population growth that might have general applicability.

5.2 Methods

5.2.1 Energy allocation model

Resource allocation in *Daphnia* was modelled by applying the thoroughly validated model by RINKE & VIJVERBERG (2005), this model is based on the partitioning of energy between somatic growth, maintenance, and reproduction (Fig. 5.1). A detailed description of the model specification is already given in chapter 4 on page 47 including a complete list of model parameters (see table 4.1). Since no population dynamics are studied here, the following analysis exclusively refers to the individual level model in section 4.3.1. Nevertheless, simulation of population dynamics would

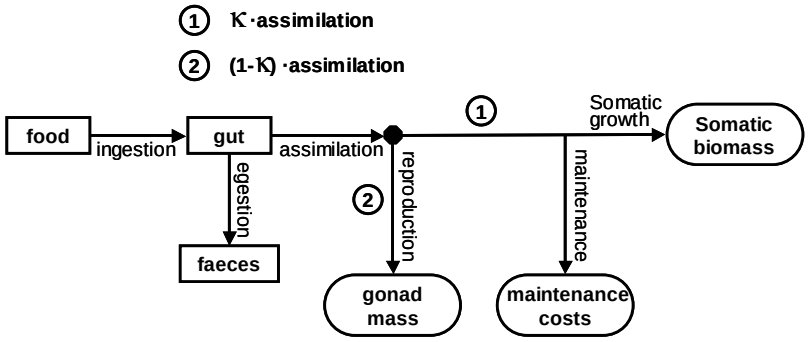

Figure 5.1: Flow chart of energy allocation in the applied energy allocation model. According to DEB-theory (κ-rule), a fixed fraction of assimilate is allocated into somatic growth and maintenance (κ) and the remaining assimilate (1-κ) is committed to reproduction/maturation.

be easily realizable by applying the population level model described in section 4.3.3.

5.2.2 Patterns in resource allocation with respect to life-history shifts

To elucidate the effect of varying allocation strategies on individual somatic growth and egg production, as a first step, the energy allocation factor κ, i.e. the proportion of assimilated carbon allocated into somatic growth and maintenance, was varied in the model. This first step aimed at the quantitative understanding of the relationship between resource allocation and individual life-history. Secondly, an examination of model predictions for reproductive effort was carried out and compared with findings from empirical observations. Studies on life-history frequently use the reproductive effort as a proxy for resource allocation towards reproduction. In a study of *Daphnia hyalina*, STIBOR (1992) calculated reproductive effort as egg production within an instar divided by the sum of somatic mass increment and egg production (both as dry weight) within this instar, i.e. reproductive effort corresponds to the percentage of net production given to reproduction. He provided empirical evidence that reproductive effort (i) increases with individual body weight and (ii) this size-dependent reproductive effort is augmented under exposure to fish infochemicals (kairomones). In order to compare model outputs with his findings, somatic growth increment and egg production per instar for a range of individual body weights was calculated. For the latter,

a carbon content per egg of 0.7 μg C (BOERSMA, 1995) was assumed. Model outputs for body size increment and egg production were further converted into dry weight by assuming a percentage of carbon per dry weight of somatic mass and eggs of 44% and 50%, respectively (HESSEN, 1990).

Previous studies have shown that life-history responses to predator infochemicals are diverse and some of these differences have been attributed to clonal diversity (BOERSMA *et al.*, 1998; DE MEESTER & WEIDER, 1999). These clonal differences were taken into account by parameterizing the model to life-history data of nine clones of *Daphnia galeata* $\times$ *hyalina* taken from DE MEESTER & WEIDER (1999). Data provided in this study were considered particularly appropriate for our model approach because: (i) they studied relevant life-history parameters of several clones, and (ii) they used preconditioned animals whose mothers have also been exposed to kairomones. The latter is important because kairomones can also affect size of neonates and one would measure a transitional state when using neonates from control animals previously not being exposed to kairomone (DE MEESTER & WEIDER, 1999). In their study, DE MEESTER & WEIDER (1999) distinguished clones showing a behavioral response to fish kairomone ('risk-averse') from those without a behavioral response ('risk-tolerant'). The latter group exclusively employed life-history shifts in response to kairomone exposure. Consequently, these nine clones comprising the risk-tolerant group were used for the analysis . Experiments of DE MEESTER & WEIDER (1999) were conducted at 20 °C and a food concentration of 1 mg C L^{-1}.

The following life-history characteristics were provided by DE MEESTER & WEIDER (1999): size at first reproduction[2] (*SFR*), size of neonates (*SON*), age at first reproduction (*AFR*), and number of eggs in first clutch (*NEFC*). Length measurements were carried out from the top of the eye to the base of the tail spine (*EL*). This length measure was converted into total body length (TL, from top of the head to the base of the tail spine) – the respective length measure in the energy allocation model – on basis of own measurements ($TL = 1.07 \cdot EL$, $r^2 = 0.998$, $n = 55$). All model parameters involved in resource acquisition and maintenance were assumed to be equal for all clones. Only two parameters had to be adapted in order to simulate observed life-histories: the energy allocation factor κ and carbon investment per egg c_E. Pa-

[2] According to the definitions given in chapter 4, *SFR* describes the size at which the first clutch of eggs are deposited into the brood chamber, whereas *SAM* is defined as the size at which gonads are becoming ripe, i.e. egg production in the gonads starts. These definitions also account for *AFR* and *AAM*, respectively.

rameter κ was estimated using Eqs. (4.19-4.21) by finding a value that satisfies the requirement to reach *SFR* at the age of *AFR* with the body length *SON* at age zero (least squares). The respective values for *SFR*, *AFR*, and *SON* were taken from DE MEESTER & WEIDER (1999). For estimating the carbon investment per egg c_E, one first has to define the size at maturity (*SAM*). As explained in chapter 4, *SAM* is defined as the size when gonads are becoming ripe and carbon is channelled into egg production. This is the case during two instars (commonly considered as juvenile or preadult instars) before eggs are deposited into the brood chamber for the first time (ZAFFAGNINI, 1987). Since a 'juvenile' instar duration is roughly half as long as adult instar duration *D* (corresponding to egg development time, BOTTRELL, 1975), age at maturity (*AAM*) is calculated from:

$$AAM = AFR - D \tag{5.1}$$

Once *AAM* is known, *SAM* can be calculated by Eqs. (4.19-4.21). Finally, total carbon in the gonads accumulated over the duration from *AAM* to *AFR* was calculated and divided by the number of eggs in the first clutch in order to achieve an estimate of c_E.

$$c_E = \frac{1}{NEFC} \int_{AAM}^{AFR} (1-\kappa) \cdot A(SAM, F, T) dt \tag{5.2}$$

The term $A(SAM, F, T)$ refers to assimilation rate, which is a function of current body size. i.e. *SAM*, and ambient food concentration (F) and temperature (T).

5.2.3 Size selective predation and population growth

Fish feeds selectively on large zooplankton prey and survival probability of the prey declines with increasing size (WERNER & HALL, 1974). In order to account for size selective feeding of planktivorous fish, a sigmoid relationship between body size and mortality rate was assumed (compare TAYLOR & GABRIEL, 1992; SPAAK *et al.*, 2000). Mortality rate *d* was calculated as a function of body length:

$$d = background.mort + deflection.mort \left(1 + \tanh\left(slope.mort(L - L_{mid})\right)\right) \tag{5.3}$$

where $background.mort$ is non-selective background mortality, $deflection.mort$ describes the deflection of the tanh-function, $slope.mort$ is the slope in the sigmoid

function, and L_{mid} depicts the point of inflection. In all scenarios a background mortality of $0.05\,\mathrm{d}^{-1}$ and a slope of 3.0 was applied, which corresponds to observations by KÖPKE *et al.* (1988). The remaining two parameters are well interpretable in an ecological sense and, therefore, were varied over a reasonable range in order to reflect different predation regimes (see Fig. 5.2). Parameter $deflection.mort$ was considered to represent the intensity of predation, thus being related to the abundance of planktivorous fish in the habitat. The parameter L_{mid} is related to the turning point indicating the size from which on prey is positively selected, i.e. per capita death rate becomes higher than mean death rate averaged over all body lengths. One might associate the value of L_{mid} with the length at which electivity indices where found to switch from negative to positive values in field studies (e.g. KÖPKE *et al.*, 1988). The smallest size class of water fleas that is positively selected by the fish depends, besides species specific differences, on ontogenetic changes in prey selection. The most dramatic changes occur in young of the year (YOY) fishes which are gape-limited during their first weeks of life and progressively feed on larger prey as they grow (WAHL *et al.*, 1993; MEHNER *et al.*, 1998b), while at the same time their total consumption may increase considerably (WAGNER *et al.*, 2004). According to several studies, YOY fish exert the major predatory impact on daphnids (MILLS & FORNEY, 1983; CRYER *et al.*, 1986). Empirical evidence thus strongly suggests that fish predation on *Daphnia* varies considerably with the season both with respect to predation intensity (represented by variation of $deflection.mort$ in our model) and size-selection (represented by variation of L_{mid}).

Finally, life-histories for each of the nine clones have been calculated by using the resource allocation model with the derived parameterization as explained above (at $20\,^{\circ}\mathrm{C}$ and $1\,\mathrm{mg\,C\,L}^{-1}$ as in DE MEESTER & WEIDER, 1999). This provided information about somatic growth and clutch size in each adult instar, with the latter being equivalent to the maternity function m_a. Survival probability l_a of the consecutive instars was calculated by integrating size-dependent mortality rate d over age a. Because body length L of individuals change with age a, time mortality rate d becomes a function of age and the survival probability can be expressed as:

$$l_a = \int_{a=0}^{n} d\big(L(a)\big)\,da \tag{5.4}$$

where n is the lifespan of the individual, which was set to a value allowing each clone to release 9 clutches over its life. Finally, population birth rate b can be numerically

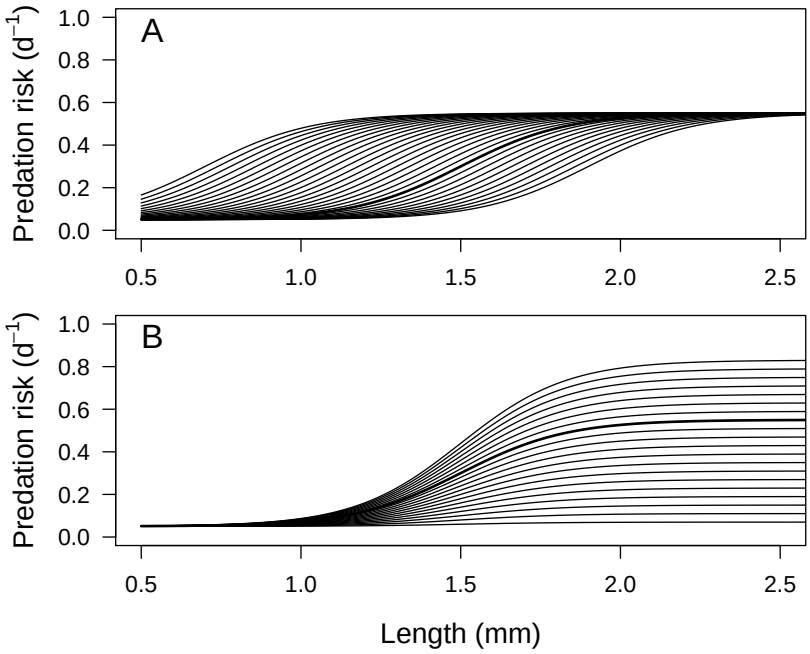

Figure 5.2: Plot of size-dependent predation risks of *Daphnia* in the predation regimes applied: the bold line depicts the standard scenario from which the different regimes were derived by varying either the predators size (**A**, i.e. selectivity for prey size) or the predators abundance (**B**, i.e. predation intensity).

derived from the Euler equation:

$$1 = \sum l_a m_a e^{-b \cdot a} \tag{5.5}$$

5.3 Results

5.3.1 Linking resource allocation to life-history

Life-history characteristics like somatic growth and age-dependent egg production are closely linked to the underlying resource allocation strategy inherent in a given *Daphnia* clone (Fig. 5.3). In this respect, the energy allocation factor κ acts as a central descriptor of metabolic organization that provides a quantitative expression of the underlying allocation strategy and, therefore, is a sensitive parameter in the determination of individual life-history. Lowering the value of κ, which corresponds to a higher allocation of resources to reproduction, i.e. the expected scenario in response to fish kairomones, resulted in reduced growth and a lower maximal body size an individual

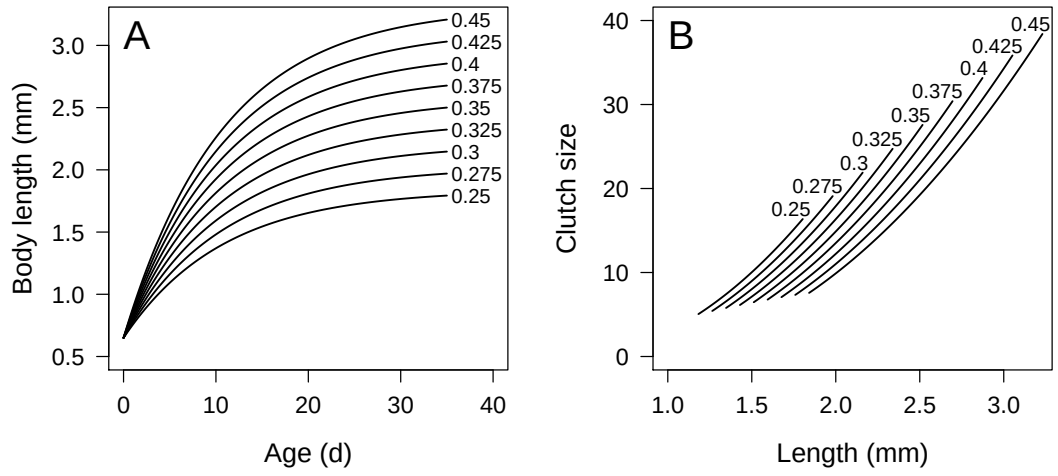

Figure 5.3: Somatic growth (**A**) and egg production (**B**) of *Daphnia* having different energy allocation strategies as reflected in the energy allocation factor κ. All other parameters correspond to the standard parameterization for *D. galeata*. Values of κ are indicated at the upper end of the lines (at 20 °C and 1 mg C L^{-1}; for effects of temperature and food concentration on life-history see chapter 4).

will potentially reach (Fig. 5.3A). Accordingly, such a strategy leads to lowered size at maturity. On the other hand, clutch size at a given length is higher because more energy is channeled into reproduction (Fig. 5.3B).

There is also a direct control of the energy allocation factor κ on reproductive effort, which by definition can be immediately calculated from the outputs of the energy allocation model. For example, lowering the value of κ from 0.32 to 0.27 in the standard parameterization for *D. galeata* resulted in a shift in reproductive effort that corresponds to observed shifts in reproductive effort of *D. hyalina* when exposed to fish kairomones (Fig. 5.4). Focusing on somatic growth, such a decrease in κ is associated with a reduction of maximal body length from 2.4 to 2.0 mm.

5.3.2 Resource allocation patterns and associated costs in observed life-history shifts

The model application to the life-history data recorded by DE MEESTER & WEIDER (1999) revealed a reduced resource allocation towards somatic growth in animals ex-

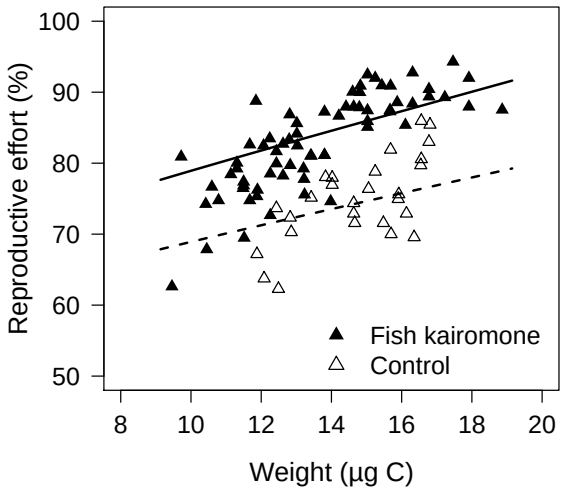

Figure 5.4: Comparison of calculated reproductive effort by the energy allocation model for different energy allocation strategies (solid line: $\kappa = 0.27$; dashed line: $\kappa = 0.32$; other parameters correspond to the standard parameterization for *D. galeata*) and reproductive effort of *Daphnia hyalina* in animals exposed to fish kairomones (black triangles) and control animals (open triangles) as measured by STIBOR (1992).

posed to fish infochemicals (Table 5.1). All nine clones showed a consistent response in the fish treatment by reducing the energy allocation factor κ when compared with control conditions (paired t-test, $p < 0.001$; n = 9, Fig. 5.5 A-B). However, although all clones showed a reaction in the same direction, the intensity of this response was rather variable and in the case of one clone even appeared to be negligible (clone 7). As a consequence of this differential response of the clones, variability of phenotypes increased in the fish treatment. Surprisingly, six out of nine clones also showed an increase in the carbon investment per egg (parameter c_E) although all clones consistently reduced the size of their offspring in the fish treatment (Fig. 5.5 C-D). Thus, only the remaining three clones showed a response in parameter c_E that is expected from the respective change in size of neonates. On average, parameter c_E was significantly increased in the fish treatments (paired t-test, p = 0.046; n = 9). This increased carbon investment per egg in the fish treatments revealed overhead costs associated with the life-history shift, which appeared to be particularly high in clones showing a strong shift in resource allocation as given by the change in energy allocation factor κ. These results point out that observed life-history shifts of *Daphnia* cannot be explained by

Table 5.1: Measured original data from DE MEESTER & WEIDER (1999), estimated parameters according to the procedure explained in the text and derived parameters calculated from these data by applying the energy allocation model.

		Measured data				Estimated parameters		Derived parameters	
Clone	Treatment	SFR (mm)	SON (mm)	AFR (mm)	SFC (mm)	κ —	c_E (μg C egg^{-1})	L_{max} (mm)	SAM (mm)
1	control	1.37	0.56	5.51	4.70	0.352	1.29	2.589	1.03
1	fish	1.26	0.55	6.14	4.01	0.296	1.53	2.175	0.99
2	control	1.38	0.55	5.64	5.25	0.352	1.18	2.588	1.04
2	fish	1.30	0.55	5.51	5.25	0.328	1.08	2.412	0.98
3	control	1.40	0.56	5.64	5.72	0.356	1.10	2.620	1.06
3	fish	1.22	0.54	6.64	3.02	0.275	2.10	2.024	1.00
4	control	1.42	0.57	5.51	4.97	0.366	1.27	2.691	1.06
4	fish	1.27	0.56	6.51	2.51	0.289	2.64	2.125	1.03
5	control	1.43	0.57	5.51	6.21	0.368	1.01	2.707	1.06
5	fish	1.24	0.54	6.51	.98	0.281	1.59	2.070	1.00
6	control	1.45	0.55	5.51	6.97	0.379	0.89	2.788	1.07
6	fish	1.28	0.52	5.34	3.00	0.334	1.73	2.455	0.94
7	control	1.49	0.57	5.38	6.71	0.395	0.94	2.907	1.09
7	fish	1.42	0.54	5.01	6.48	0.394	0.82	2.898	1.00
8	control	1.49	0.55	5.38	6.71	0.400	0.92	2.946	1.08
8	fish	1.28	0.50	4.89	5.25	0.357	0.86	2.627	0.89
9	control	1.50	0.57	5.26	6.97	0.403	0.89	2.963	1.08
9	fish	1.40	0.55	5.14	5.74	0.377	0.97	2.774	1.01

a shift in resource allocation alone because in most clones additional energetic costs have been detected in the fish treatment.

To unravel the consequences of these costs on the bioenergetic level for the population, the model outputs were used to calculate population growth rates for all clones and treatments under the assumption of a constant background mortality of 0.05 d^{-1} (i.e. no size-selective predation). These population growth rates varied over a considerable range (0.17 - 0.32 d^{-1}) and this variability was not attributable to external factors like resource level or temperature but only to phenotypic plasticity. In fact, seven out of nine clones realized a reduced population growth rate in the fish treatments. If the calculated population growth rates were compared with the respective energy allocation factor κ, it emerged that there is a trend to higher growth rates with increasing κ, which is reflected in a high correlation between these two measures ($r^2 = 0.88$, $p < 0.001$, n=18, fig. 5.6A). Consistently, there was also a significant negative correlation between population growth rate and the carbon investment per egg

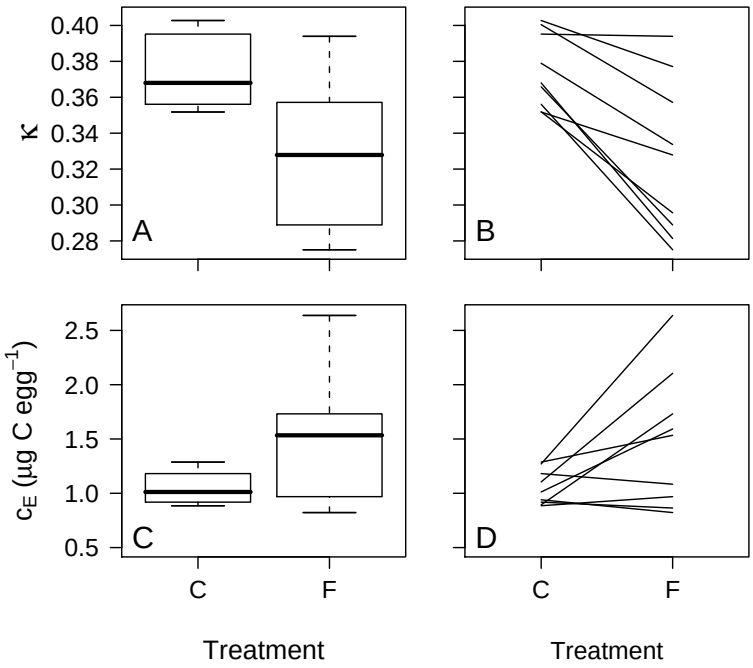

Figure 5.5: Evaluation of the somatic growth displayed by the 9 clones in DE MEESTER & WEIDER (1999) with the energy allocation model. Boxplots (A) and clone-specific responses (B) of the energy allocation factor κ in both groups of treatments. Figures C and D show the respective responses in the parameter c_E (carbon investment per egg); treatments: F = animals exposed to fish kairomone; C= control animals; n = 9; boxplots mark median, first and third quartile and range of the data.

($r^2 = 0.92$, $p < 0.001$, n=18, fig. 5.6B) reflecting the consequences of the costs on the bioenergetic level. These results indicate that such clones that reduce their somatic growth to a very low level in response to fish kairomones, i.e. realizing a low κ, do suffer elevated costs on the bioenergetic level, i.e. having a high carbon investment per egg, that lead to a severely reduced population growth rate under conditions of non-selective predation.

5.3.3 Adaptive value of life-history shifts

In order to explore whether the observed life-history shifts are adaptive under positive size-selective predation, population growth rates were calculated for all clones and for both life-history strategies per clone under a range of possible predation regimes. For this purpose, either the midpoint (analogous to variation in size-selection) or the deflection (analogous to predation intensity) of the sigmoid function of predation risk

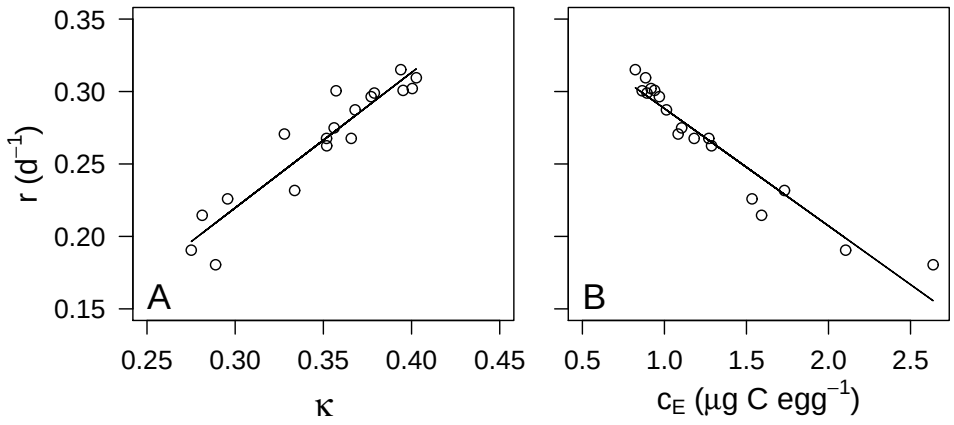

Figure 5.6: (A) Linear regression between energy allocation factor κ and the population growth rate r of each clone and treatment as calculated by the model ($y = 0.93x - 0.06$, $r^2 = 0.88$, $n = 18$, $p < 0.001$). Separate linear regressions calculated for fish and control animals were not significantly different from each other (ANCOVA, p (slope) = 0.20, p (interc.) = 0.35). (B) Linear regression between parameter c_E and the population growth rate r of each clone and treatment as calculated by the model ($y = -0.08x + 0.37$, $r^2 = 0.92$, $n = 18$, $p < 0.001$). Separate linear regressions calculated for fish and control animals were not significantly different from each other (ANCOVA, p (slope) = 0.47, p (interc.) = 0.28).

(see Fig. 5.2) was varied while keeping the other factors constant. Population growth rates decreased with increasing predation intensity and with progressive selection of smaller individuals (Figs. 5.7 & 5.8). Due to the large phenotypic variability of the clones their performance in the predation scenarios differed considerably from each other.

On the whole, one can categorize the clones into three classes according to their response to predator infochemicals. For three clones (No. 2, 7 and 8) the observed life history responses to fish infochemicals were found to be always adaptive, i.e. the population growth rate was always higher in the presence of fish, no matter which predation scenario was applied. These clones were found to have no or negligible costs arising from the life-history shift. They even reduced their carbon investment per egg in the fish treatment, which means that no overhead costs on the bioenergetic level have been detectable. In a second group of clones (No. 3, 4 and 6) quite the opposite was observed and life history responses to fish were hardly adaptive since r was found to be higher for the life-history displayed under control conditions (midpoint scenario, see Fig. 5.8). However, in the deflection scenario the lines of r of both life-history

strategies did cross at high predation intensities for these clones, indicating that under very intense predation the life history shifts did effectively become adaptive (Fig. 5.7). Costs of life history shifts in these clones are considerable, which is reflected by the fact, that the carbon investment per egg is roughly doubled in the fish treatments. In a third group of clones (No. 1, 5 and 9) an adaptive advantage of fish-induced life history shifts can be found under specific predation scenarios. Here the lines of *r* cross both in the midpoint and in the deflection scenarios at least once within the range

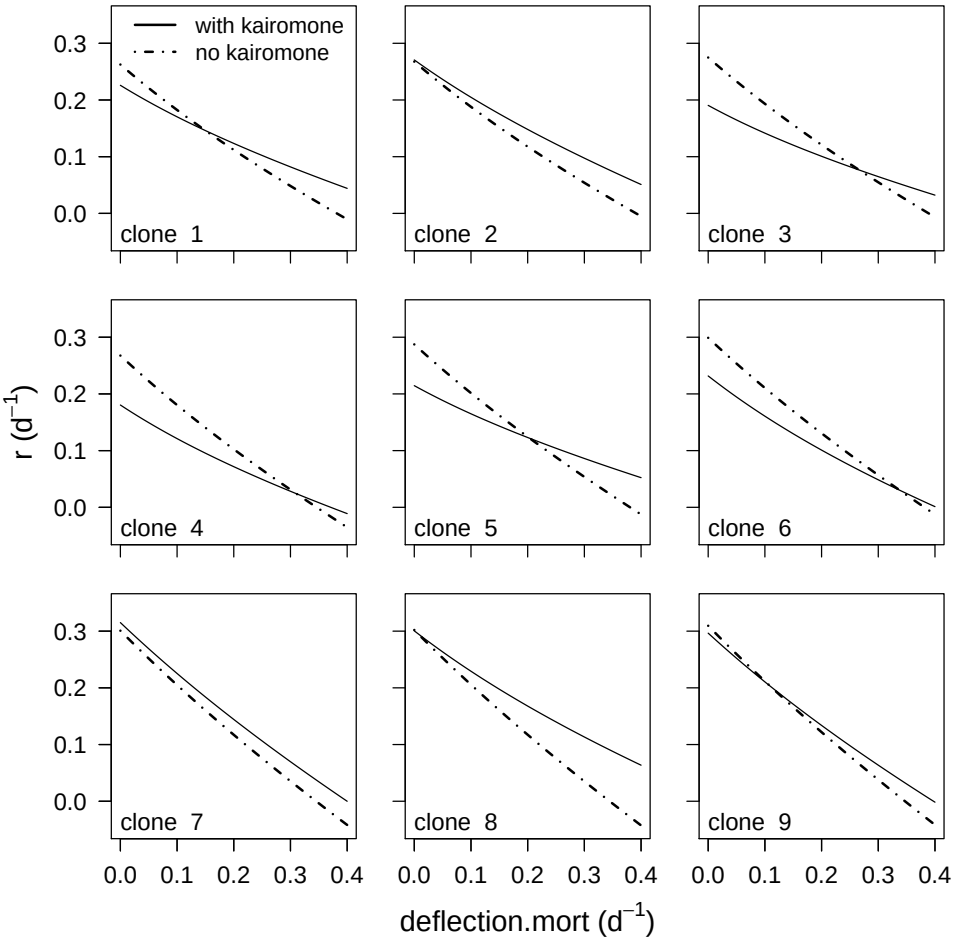

Figure 5.7: Clone-specific population growth rates *r* at varying predation intensities as displayed by the predation model parameter *deflection.mort*. A value of zero for *deflection.mort* corresponds to non-selective predation. Lines represent different life-history strategies of the clones: either the life-history expressed in control treatments (no kairomone, dashed line) or the life-history expressed in fish treatments (with kairomone, solid line).

of parameters applied. The induced life-history is already adaptive at intermediate predation intensities and, thus, costs can be categorized as being intermediate, which again is indicated by a moderate increase of the parameter c_E in the fish treatments.

The fitness consequences of fish-induced life history shifts generally were less sensitive to variations of the midpoint of the predation function than to variations in deflection. In those clones where life history responses were always or never adaptive variation of the midpoint had obviously no influence on the outcome of our analysis. Only in three out of nine clones did variation of the midpoint of the predation model

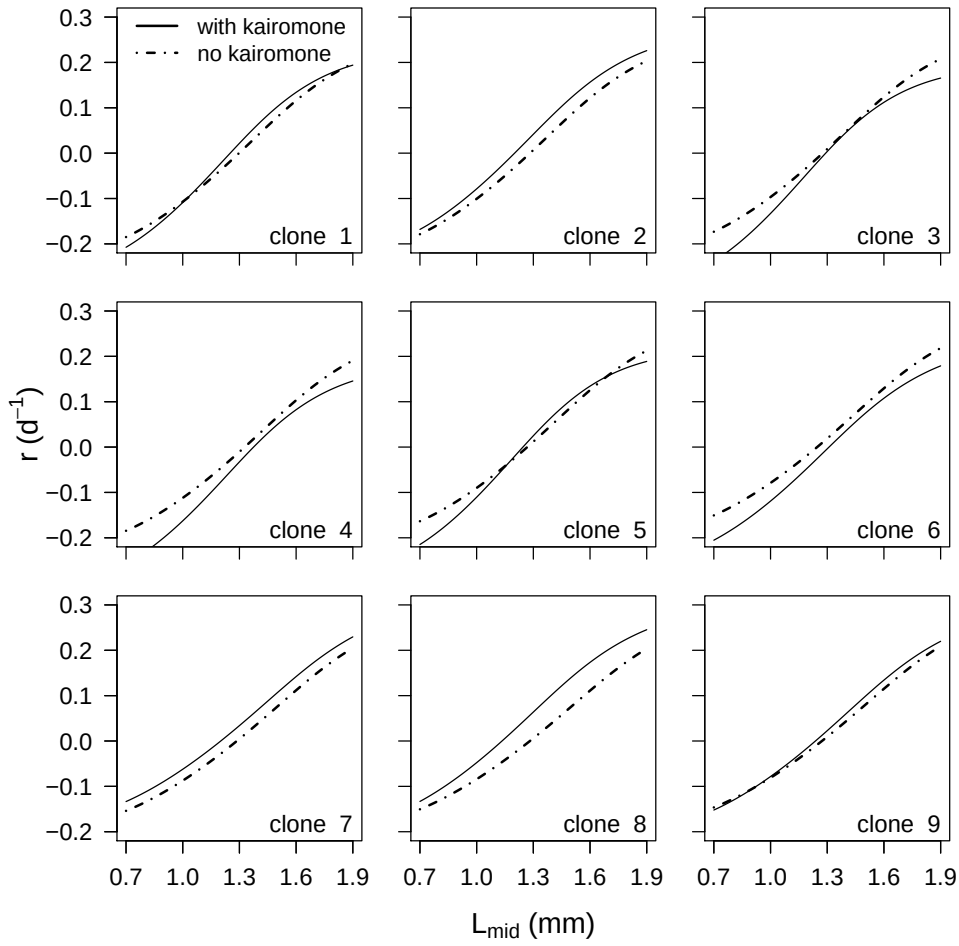

Figure 5.8: Clone-specific population growth rates *r* at varying size selection behavior of the predator as displayed by the predation model parameter L_{mid}. Lines represent different life-history strategies of the clones: either the life-history expressed in control treatments (no kairomone, dashed line) or the life-history expressed in fish treatments (with kairomone, solid line).

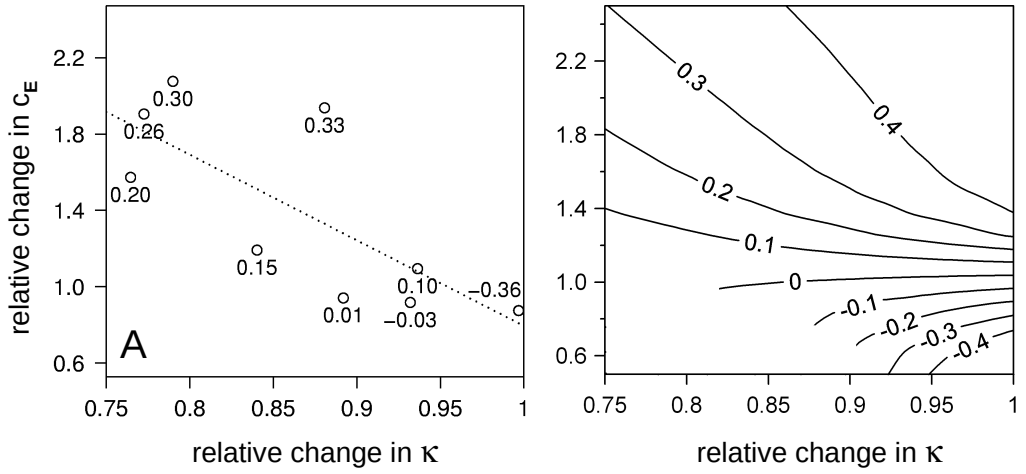

Figure 5.9: (A) Relative changes in the energy allocation factor κ and the carbon investment per egg c_E of the nine *Daphnia*-clones in response to fish kairomone (points) and the corresponding linear regression (dotted line, $y = -4.49x + 5.28$, $p = 0.02$, $n = 9$). Numbers close to data points indicate the critical predation intensity, i.e. surpassing this critical predation intensity turned the life-history shift to become adaptive. (B) Critical predation intensities (isolines, d^{-1}) of an average individual calculated from a simulation study over a range of possible life-history shifts as defined by the respective relative change in the parameters κ and c_E over the trait space covered by the nine *Daphnia*-clones.

turn an advantageous life history shift into a disadvantage or vice versa. Note, however, that midpoints < 1.2 mm generally resulted in population declines within the chosen parameter range.

These results show that the observed life-history shifts of most *Daphnia*-clones appear to be associated with overhead costs on the bioenergetic level. In consequence, a distinct size-selective predation intensity is necessary that these costs do pay off. This critical predation intensity necessary to turn the life-history shift to become adaptive varies between clones and scale with the extend of the overhead costs (Fig. 5.9A). Particularly such clones that showed a strong reduction of the energy allocation into somatic growth, i.e. lowering κ significantly, on average also suffered higher overhead costs, and therefore realized an adaptive value of their life-history shift only under rather high predation intensities. There is, in fact, a trade-off between changing the resource allocation by reducing κ, i.e. to minimize the effective predation window on the population by reducing somatic growth, and emerging overhead costs as expressed in an increased carbon investment per egg. In order to draw a more generalized picture of this trade-off, the trait-space realized by the nine clones was extensively evaluated

by a simulation study. This was done by defining an average individual from the control animals in DE MEESTER & WEIDER (1999) and simulating different possible life-history shifts of this average individual by applying different relative changes in the parameters κ and c_E. Finally, for all these life-history shifts the critical predation intensity having equal population growth rates for both life-history strategies was calculated. The emerging pattern showed that strong changes in resource allocation do only pay off if size-selective predation in the environment is intense. However, there is still a large region in the trait space where a life-history shift is not costly and always adaptive under size selective predation. This region is restricted to such clones that reduce their κ by not more than ca. 10-15 % when exposed to fish kairomones as indicated by the isoline for a critical predation intensity of zero, which separates costly (above this isoline) from non-costly life-history shifts (below this isoline). However, the fact that the majority of clones realized a costly life-history shift indicates that in the environment of these clones such high predation intensities are prevailing.

5.4 Discussion

5.4.1 Bioenergetics of life-history shifts

This study gives strong support to the hypothesis that predator-induced phenotypic life history responses result from a shift in the underlying resource allocation as represented by the parameter κ in the applied model. It is suggested that in response to fish kairomones the allocation of resources to somatic growth is decreased (by reducing κ), resulting in slower somatic growth, reduced size at maturity and an increased reproductive effort, which corresponds to empirical observations (e.g. STIBOR, 1992). In fact, principal shifts in most life-history traits commonly observed in experimental and field studies, e.g. size and age at maturity, reproductive effort, or somatic growth rate, may all arise from the same basal switch in metabolic organization that is reflected by the parameter κ. However, by using observations of life-history shifts in nine clones of *Daphnia* for a quantitative evaluation of the underlying resource allocation pattern it explicitly emerged that a change in the energy allocation factor κ was only in three clones sufficient to explain the observed life-history shifts. In the remaining six clones, besides a change in κ, considerable costs on the bioenergetic level have been detected that appeared to be associated with the life-history-shift. Since the

costs rise when a strong shift in the energy allocation takes place this finding reveals a trade-off involved in the life-history shift. These costs became only quantifiable due to the methodology of this study to model the life-history by means of a closed energy budget and provide an explanation why the defense is inducible. The application of resource allocation models, therefore, provides a unifying framework for the research associated with life-history variation, phenotypic plasticity and the evolutionary processes involved therein. Such models do not only account for shifts in resource allocation and facilitate the quantification of potentially associated overhead costs; they even enable to interpret the consequences of all these individual level processes in terms of fitness and by this allowing an interpretation in an evolutionary context.

Within this framework, the energy allocation parameter κ provides the quantitative expression for the underlying shift in resource allocation of an observed life-history variation. The pioneering work on dynamic energy budget models by KOOIJMAN, who firstly introduced the κ-rule, by using a strain of *Daphnia magna* revealed κ to vary in the range between 0.30 and 0.33 (KOOIJMAN & METZ, 1984; KOOIJMAN, 2000). In this study κ was found to vary in a slightly broader range from 0.28 to 0.40, which has to be attributed to genetic variation and phenotypic plasticity of individuals involved in this analysis, but still rather closely matches the values provided by Kooijman's group. In addition, the standard parameterization ($\kappa = 0.35$) of the model used in this study was proven to describe life-history variation under different conditions of food concentration and temperature quantitatively correct (RINKE & VIJVERBERG, 2005). Nevertheless, the assumption to model resource allocation with a constant is not easy to support from an empirical perspective because we lack the opportunity to track the involved processes (ingestion, assimilation, tissue growth, embryogenesis etc.) over an individuals lifespan. However, recent experiments by MIKULSKI *et al.* (2004) support the assumption that principal energy allocation is rather fixed for an individual and is determined early during an individuals ontogeny. They studied the resource allocation in *Daphnia magna* by exposing individuals of different age to fish infochemicals and found that only newborns switched their resource allocation strategy while older individuals did not. Furthermore, the quantitative agreement between model predictions for reproductive effort and measurements on *Daphnia hyalina* (Fig 5.4) supports the application of a constant energy allocation factor over an individuals lifetime. Concerning this model output it is important to note that reproductive effort increases with body size despite κ being a constant. This is because the model explic-

itly accounts for maintenance costs that compete with somatic growth for resources and increase faster with body size (they scale with L^3) than resource acquisition rate (which scales with L^2): the larger an individual would be the more energy is needed to meet maintenance and therefore less resources are available for somatic growth.

5.4.2 Costs of induced life history shifts and adaptive value

In six out of nine clones the life-history shift in response to fish kairomones was associated with overhead costs. As a consequence of the applied model parameterization procedure these costs are reflected by an increased carbon investment per egg (parameter c_E). In fact, the employed application is able to quantify these costs on the bioenergetic level but is not suited to exactly localize the physiological process that caused the costs. It might be that alternative processes are the ultimate cause of the costs, e.g. a lower resource acquisition rate, less efficient digestion or additional losses in anabolic processes. Variations in resource acquisition rate could potentially account for fitness variation between clones (REZNICK *et al.*, 2000). However, comparative physiological investigations have found individual rates of ingestion, assimilation and respiration not to be affected by kairomones and therefore unrelated to induced life history shifts (TOLLRIAN, 1995; STIBOR & MACHACHEK, 1998). But nevertheless, one can hardly draw final conclusions from these findings since each of the studies were performed on a single *Daphnia*-clone and from this study we know that the overhead costs do not necessarily arise in all clones. In this respect it is not surprising that RAMCHARAN *et al.* (1992) indeed found a reduced ingestion rate in *Daphnia pulex* when exposed to kairomones from *Chaoborus*-larvae. Although it remains uncertain wherefrom the bioenergetic costs in the fish treatments really originated, this approach provides the methodology to detect and quantify these costs. Note also that another way of parameterization would lead to a different localization of these costs, e.g. in terms of a reduced ingestion rate in the fish treatment, but would not lead to different conclusions about underlying resource allocation patterns (e.g. a reduced investment in somatic growth in the fish treatments) or the adaptivity of the observed life-history shifts.

In an environment without size-selective predation the fish-induced life-history on average yielded a lower population growth rate than the corresponding life-history in the absence of fish. This was explicitly the case in seven out of nine clones and reflects the costs of the induced life-history shifts for these clones. To a large ex-

tend these costs on the population level arise from the overhead costs detected on the bioenergetic level. A second cause of costs is the reduced somatic growth in the fish treatments since net production of *Daphnia* is strongly size-dependent (e.g. LYNCH *et al.*, 1986) and a lowered somatic growth will therefore reduce net production in future. In consequence, a certain intensity of size-selective predation has to be surpassed in order to turn the life-history shift to become adaptive. In principle, this result corresponds to the theory of inducible defenses, which states that defenses are costly and therefore not continuously expressed (HARVELL, 1990; TOLLRIAN & HARVELL, 1999).

However, in two clones costs for the defenses seemed to be negligible and defenses were even advantageous anyway, which contradicts theoretical predictions. It was further shown that there exists a large region in the trait space where no costs of the life-history shift occurred (Fig. 5.9). The phenomenon of no apparent costs of induced life history shifts is puzzling and immediately leads to the question why these defenses are inducible and not continuously expressed. The most likely explanation is that there are further trade-offs involved in this life-history shift which were not taken into account sofar but which have played an important role in the evolution of this defense. One can only speculate about this issue, but I would like to propose the following trade-offs to be possibly of importance for the observed life-history shifts. Firstly, since *Daphnia* reduced the size of their offspring in the fish treatments (Table 5.1), neonates suffer reduced hatching success and juvenile survival. Survival of neonates was found to be positively correlated with egg size and size of newborns (BELL, 1983) and large offspring were proven to be more resistant to stressors like starvation (GLIWICZ & JACHNER, 1992; CLEUVERS *et al.*, 1997; STIBOR & MÜLLER-NAVARRA, 2000). Secondly, a reduction of the energy allocation factor κ implies not only slower somatic growth and a reduced maximal body size but also less energy available for maintenance. In an analysis aimed on the calculation of minimal food requirements (R* according to TILMAN, 1982) for different *Daphnia* species, HÜLSMANN *et al.* (2005) showed that such a reduction of κ is associated with an increased minimal food requirement. It therefore could be hypothesized fish induced life-history shifts making the individuals less competitive for food. Thirdly, vulnerability of individuals to predators with different size preferences in the environment is increased (TOLLRIAN, 1995). To slow down an individuals somatic growth would be costly when predation turns out to be negatively size-selective, which is typically the

case when invertebrate predators like *Chaoborus* or *Leptodora* are abundant (LYNCH, 1979). Therefore, in environments with alternating predation regimes or where fish and invertebrate predators coexist, which has been reported for different water bodies (e.g. STIBOR & LAMPERT, 2000; WAGNER *et al.*, 2004), a life-history shift towards slower somatic growth is harmful. A similar situation might arise when juvenile fish, which are still gape-limited, are the main predators of *Daphnia* (MEHNER *et al.*, 1998a,b). Since daphnids do not differentially respond to fish, which are gape-limited or not, the induced life history shifts indeed may be maladaptive. However, due to interactive effects of food conditions and kairomone exposure the costs associated with this mismatch between induced response and actual predation threat were supposed to be low (HÜLSMANN *et al.*, 2004).

From the fact that life history shifts in single clones turn into an adaptive advantage at quite different predation scenarios, especially with respect to predation intensity (critical predation intensity), one should expect a different sensitivity to fish kairomones. Although it is known that *Daphnia* clones differ in general responsiveness to infochemicals (BOERSMA *et al.*, 1998) and that the strength of the responses depends on the concentration of the kairomone (REEDE, 1995), I am not aware of any study demonstrating differing thresholds of responsiveness to kairomones in different clones. Differential sensitivity to kairomones may also be probable since the information derived from the kairomone is always associated with a distinct uncertainty: the response is not directly related to the ultimate factor, i.e. in our case to size selective predation. The example *Daphnia*-fish in this context is of particular interest because the daphnids cannot differentiate between different fish species (VON ELERT & POHNERT, 2000). Consequently, not all kairomone in the environment necessarily has to stem from planktivorous fish. Alternatively, such kairomones could potentially be released by large predatory fishes, which of course would not exert positive size-selective predation on *Daphnia*. Hence, *Daphnia* clones from lakes differing in the structure of their fish community may have different responsiveness to fish cues. However, such a variable responsiveness would also promote the evolution of different critical predation intensities as observed in this study. This, of course, presumes that the predation intensity in the original habitat of a given clone at least sometimes surpasses the critical predation intensity of that respective clone.

In conclusion, the framework presented in this study proved to be a suitable tool to investigate resource allocation patterns underlying predator-induced life history shifts

and to quantify costs and benefits associated with this induced defense. As far as known to the author, this is the first study that puts resource allocation, energetic costs and adaptive value of predator induced life-history shifts - using empirical data - into one solid theoretical framework. Further applications of the methodology presented here should be used to study the performance of the respective clones at different food concentrations, or even better, in dynamic simulations that include the food dynamics (for technical details see RINKE & VIJVERBERG, 2005). With 9 coexisting clones and a variety of conceivable predation regimes the number of possible model scenarios is virtually countless. The most promising approach would thus be to adopt a well defined scenario from a field study, which provides information about the life history strategies and the frequencies of coexisting clones as well as about the predominating predation regime in the environment.

6 General Discussion

This thesis provides a comprehensive and thoroughly validated model system for individual and population level dynamics of *Daphnia*. The underlying concept of this approach is considered to be 'species-oriented', i.e. independent of a specific problem or a distinct model application to a well-defined research topic. Instead, the whole model system is aimed on providing a nested, prototype-like framework with multiple possible interfaces in order to allow its application to diverse exercises in applied and basic limnology. The model structure is open for extensions and further modifications by other scientists who may adapt this system for their own purposes. Its architecture enables a direct coupling of this model system to other ecological models. Particular attention is payed to interactions between the individual level and the population level, e.g. mediated by life-cycle characteristics or demographic effects. Moreover, physiological properties of individuals are taken into account enabling a mechanistical concept for modelling individual life-history on basis of a closed carbon budget of the individual. In general, special emphasis is given to a thorough validation of model outputs on independent empirical data, which ensures a quantitative interpretation of any model application.

An example documenting the advantages of a species-oriented model framework has been given in chapter 5. The model system was used to explore the link between physiological properties of an individuals metabolic organization and the respective phenotype of the individual. Phenotypic variation, as commonly observed in life-history shifts of *Daphnia* in response to predator cues, has been explained by a shift in the underlying resource allocation strategy. Furthermore, empirical data from nine clones enabled a quantitative analysis of underlying physiological processes involved in observed life-history shifts. All clones showed a consistent response in their resource allocation strategy but individual responses differed in their intensity and the nine clones covered a broad trait space of possible responses. By applying size-selective mortality regimes it was even possible to investigate the adaptive value

of the observed life-history shifts by calculating population growth rates. In conclusion, this application of a species-oriented model system documented its specific advantages: (i) the model system links information from different levels of biological organization spanning from physiological processes over individual life-history towards the population level, (ii) it allows a quantitative interpretation of model outputs enabling scientists to comprehensively investigate trade-offs and their evolutionary context, (iii) a specific analysis can be easily expanded or linked to other research topics. In this case, for example, the effect of ambient food concentration on the adaptive value of life-history shifts can be investigated or consequences of life-history shifts on consumer-resource dynamics may be explored.

6.1 Alternative species-oriented approaches

Two different approaches to a species-oriented model system for *Daphnia* have been developed in this thesis. In a first step (chapter 3), an empirical approach was developed whereas chapter 4 deals with a mechanistical model based on energy allocation rules. Consequently, these alternative approaches differed substantially from each other in terms of their methodology. However, regarding their quantitative outputs both approaches are expected to produce comparable results.

6.1.1 Similarities and dissimilarities between approaches

Differences between both approaches are considerable on the technical level. Whereas the approach in chapter 3 uses a multiple regression model fitted on empirical data to calculate individual life-history, the competing approach in chapter 4 is based on a mechanistical energy allocation model that includes a complete carbon budget, physiological processes and a feed-back on the resource density. The second approach is more complex and takes properties and processes explicitly into account that are viewed as a 'black-box' in the first approach. In the empirical approach an individual based model was used to perform dynamic simulations on the population level. In contrast to this, population level dynamics of the mechanistic model (chapter 4) were simulated by a physiologically structured population model. But nevertheless, regarding their model outputs both approaches produce comparable quantitative results for important characteristics like minimal food requirement, maximal body length or

Table 6.1: Quantitative comparison of characteristic model outputs, either calculated by the empirical model (chapter 3) or by the energy allocation model (chapter 4).

Model output for	Unit	Empirical model (chapter 3)	Energy allocation model (chapter 4)
maximal body length	(mm)	2.40	2.50
minimal food requirement	($mg\,C\,L^{-1}$)	0.05	0.04
maximal birth rate	(d^{-1})	0.30	0.32

maximal population birth rate (Table 6.1). This indicates both approaches being rather interchangeable to each other in terms of their outputs.

Despite clear differences in their technical realization both approaches can, however, be categorized as being derived from the same prototypic model structure (Fig. 6.1). Both include a distinct individual level model delivering necessary information from the individual level (somatic growth and egg production) and a certain methodology to assign these model outputs to the population model. In the first approach, an individual based model is used and in the second approach a structured population model. The latter implies the aggregation of individuals into cohorts, which finally leads to a more efficient simulation of population dynamics. However, it is important to note that both simulation approaches are interchangeable, i.e. one might use the energy allocation model within an individual based simulation for specific purposes or, the other way round, the empirical growth model with an escalator boxcar train formulation. The system of choice depends on the specific model purpose; each of both offering certain advantages and disadvantages.

6.1.2 Advantages and disadvantages of both approaches

If a given approach turns out to be advantageous almost always depends on the intended application in mind of the user. Therefore, the advantages and disadvantages discussed below may be somewhat arbitrarily — however, they can provide a guideline for potential users to decide, which of the approaches is more suited for solving their respective problem.

The empirical approach in chapter 3 is easy to apply, no differential equations have to be solved and all calculations can be done without particular knowledge about numerical techniques. Since its computational demand is minor such an approach is well-suited for individual based simulations, in particular for computation intensive applications in spatial ecology (e.g. diel vertical migration of *Daphnia*, see RINKE

& PETZOLDT, 2002) or in simulations with large populations. Such large populations may be applied if certain traits of the model organisms are associated with a high variability or if competing ecotypes or morphotypes are simulated. However, the empirical approach is not suited for modelling the feed back of *Daphnia* on its resources. Consequently, no density-dependent processes can be taken into account and ambient food concentration is needed by the model as an input (which not necessarily means that food has to be constant in time). In contrast to this does the mechanistical approach given in chapter 4 explicitly account for density dependence via a feed back on resource density. This approach, therefore, is particularly suited to study consumer-resource dynamics. Its ability to simulate density-dependence is achieved by accounting for relevant physiological processes (ingestion, assimilation, maintenance), which opens another field of possible applications. In conclusion, only the mechanistical approach provides a framework spanning from physiological processes over the individual level towards the population.

One might argue that all simulations the empirical approach is capable of, could also be done by the mechanistical approach. Consequently, the empirical approach should be viewed as being obsolete. However, due to its increased computational demand the application of the mechanistical approach may be unsuited for specific

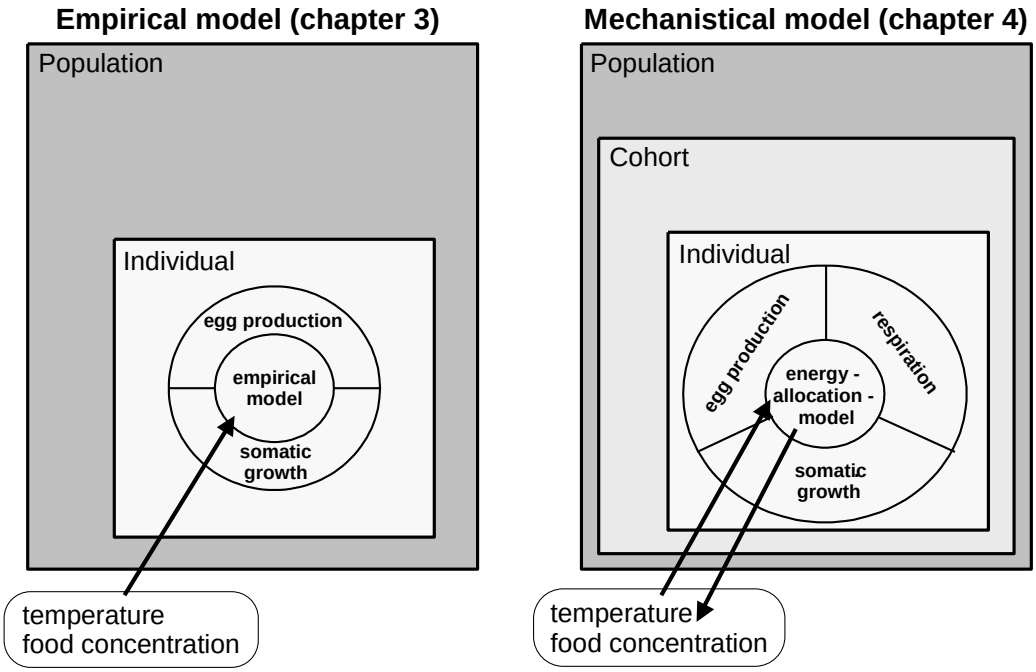

Figure 6.1: Comparison between the two model approaches of *Daphnia*.

purposes as already indicated above. Besides this, another fact should be taken into account: a mechanistical energy allocation model requires very detailed information about underlying physiological processes. Of course, such information are available for *Daphnia* but probably will be hardly available for most other organisms. Thus, the empirical approach in chapter 3 may also provide a convenient example how to model individual level dynamics of an organism without having detailed information about its physiology.

6.2 Complex transient dynamics on the population level

Observed dynamics of field populations of *Daphnia* are complex and classical unstructured population level models failed to reproduce these patterns. In this respect, the particular importance of demographic effects has already been stressed in the second chapter (see page 9) and it was a basic motivation of this work to provide a model framework where individual level processes potentially interact with population dynamics. Indeed, the population dynamics achieved by dynamic simulations with the structured population model showed different patterns in population dynamics than classical population level models (chapter 4). However, it should be noted that this comparison was carried out by using a model run of the structured population model

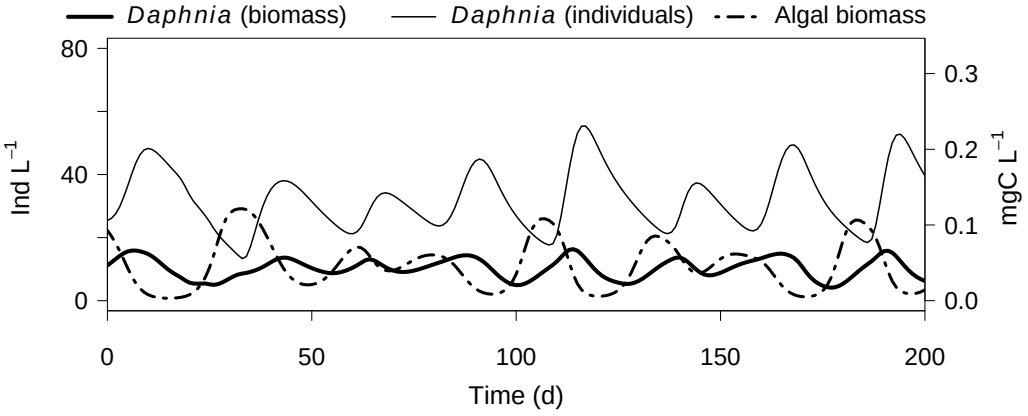

Figure 6.2: A time series of a simulation run showing transient dynamics of the consumer-resource dynamics (algal carrying capacity: $0.2\,\mathrm{mg\,C\,L^{-1}}$, max. algal growth: $1\,\mathrm{d^{-1}}$, lifespan: 30 d, temperature: 17.5 °C, all other parameters according to the standard parameterization).

in which the dynamics almost immediately converted to the asymptotic model behavior (limit cycles of consumer and resource). Such a rapid convergence towards the asymptotic model behavior is characteristic for simulations with high carrying capacities and regrowth rates of the algal resource, and for simulations with rather low mortality rates. However, in systems with elevated loss rates or less enrichment a prolonged period of transient dynamics frequently occur. An example of typical transient dynamics is given in Fig. 6.2. There are still cyclic oscillations in the abundance of consumer and resource but amplitude and frequency of the oscillations are quite variable. Depending on starting values and model parameterization these transient state can persist for long periods of a simulation (e.g. about 1250 days in the simulation shown in Fig. 6.3).

Transient dynamics of model simulations have been seldom in the scope of modelling studies. They normally depend strongly on the initial conditions of a simulation and hence it is somewhat arbitrary to focus on these dynamics. Still most theoretical ecologists prefer to study equilibrium conditions or asymptotic model behavior, which can be nicely done with classical population level models (e.g. see KRETZSCHMAR *et al.*, 1993; NORBERG & DEANGELIS, 1997; VOS *et al.*, 2004). However, there are good reasons to question whether the outcomes of such studies are really relevant for the dynamics that we observe in the real world. Non-linearities in species-interactions, seasonality, short-term variability of environmental factors, spatial heterogeneity, internal chaotic attractors and other factors force most real systems to stay far from equilibrium (HUTCHINSON, 1961; CASWELL, 1978; HUISMAN & WEISSING, 1999; HASTINGS, 2001; SCHEFFER *et al.*, 2003) and already in 1988, HASTINGS argued to focus on transient dynamics in order to improve our understanding of observed population dynamics. He also pointed out to introduce additional structures into existing models, e.g. spatial structure or age structure, and disregarded classical, unstructured Lotka-Volterra-like models. This thesis follows this line of reasoning and clearly indicates that age structure and physiological properties of a given population can lead to prolonged transient dynamics.

Transient dynamics potentially show chaotic behavior (transient chaos, see HUISMAN & WEISSING, 2001). In the seminal work of HUISMAN & WEISSING (1999) it was shown that already rather simple consumer resource models tend to behave like chaotic systems and hardly reach an equilibrium state. In their model no external forcing factors like seasonality or spatial heterogeneity were necessary to invoke

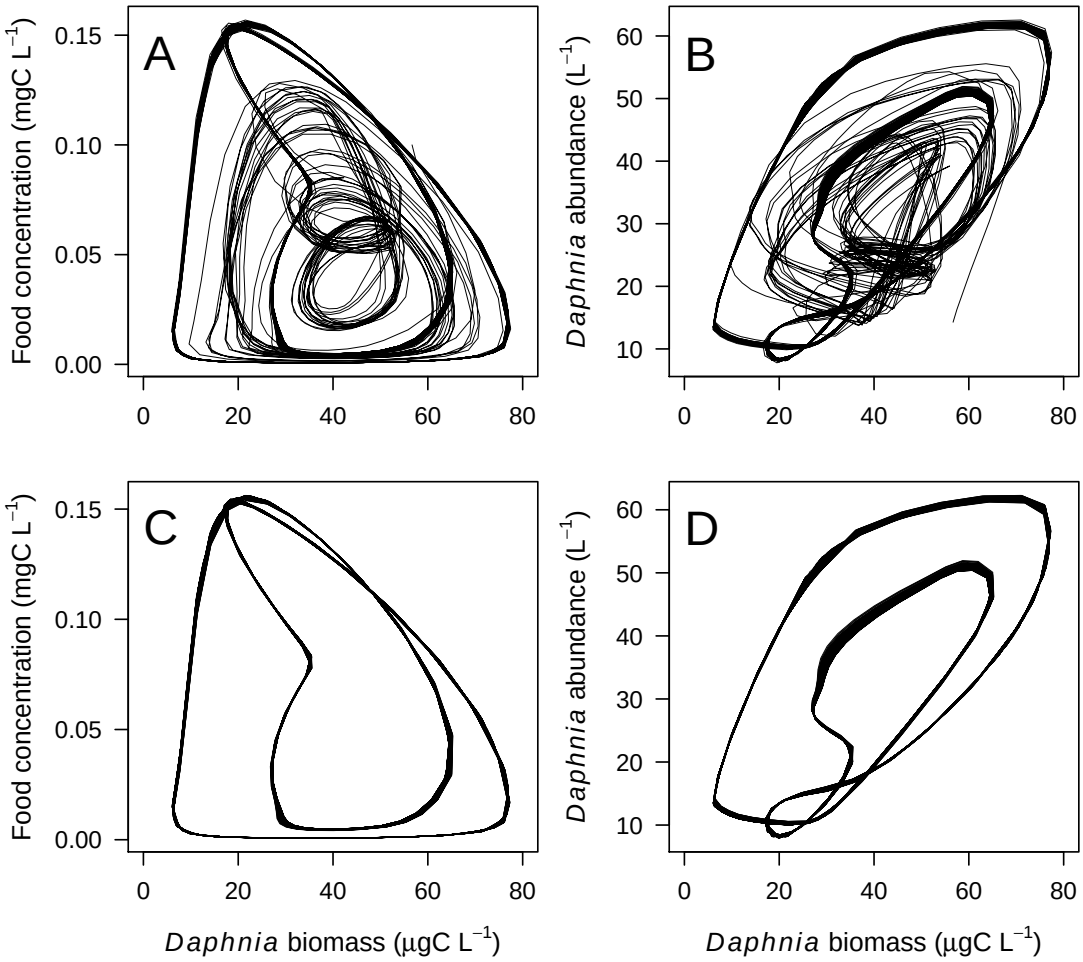

Figure 6.3: State diagrams of a simulation performed with the physiologically structured population model (chapter 4) for a period of 10000 days (algal carrying capacity: 0.2 mg C L^{-1}, temperature: 20 °C, all other parameters according to the standard parameterization). State diagrams are drawn either for the whole simulation period (A & B), i.e. including the transient dynamics, or only for that simulated period showing asymptotic limit cycles (C & D; starting from day 1300). Depicted state variables are indicated as axis annotations.

the chaotic behavior and, therefore, the chaotic dynamics appeared to be an intrinsic characteristic of such biological systems. This fact has finally led to the conclusion that there is a fundamental unpredictability of the dynamics of planktonic communities (HUISMAN *et al.*, 2001). The model system presented in this thesis represents a two-species approach (algae, *Daphnia*). However, due to the subdivision of the *Daphnia*-population into distinct cohorts and the fluctuating demography over time this system can also display transient chaotic behavior. If a given simulation is repeated

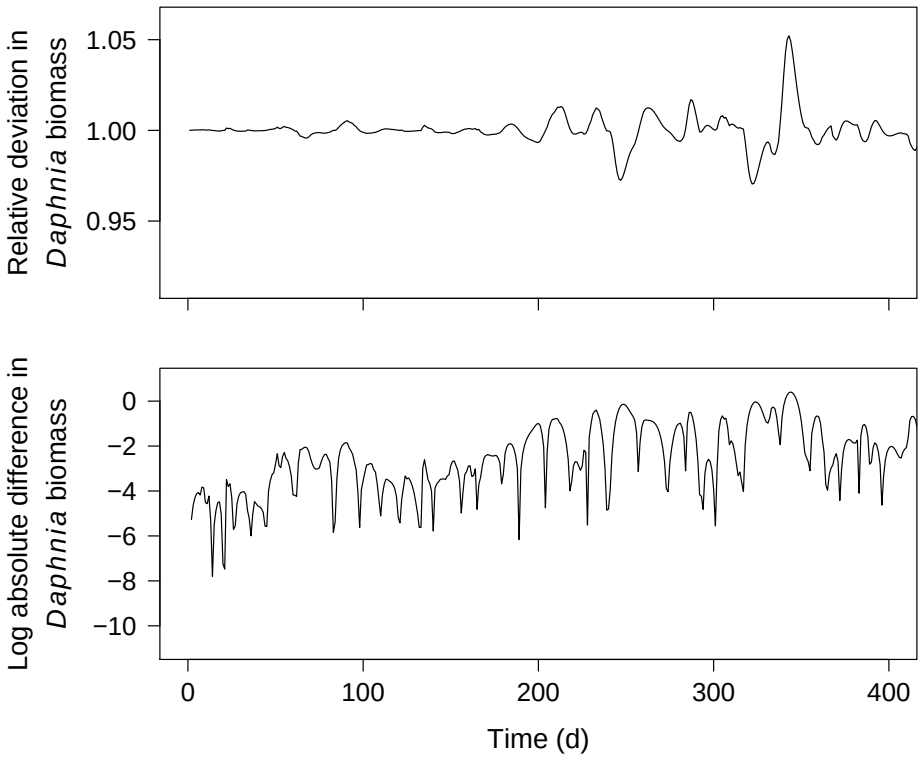

Figure 6.4: Deviations in *Daphnia*-biomass between two simulations with slightly changed initial values for the food concentration are drawn as time-series (absolute difference in the initial value of the food concentration: 10^{-4}). The relative deviation (upper panel) as well as the absolute deviation (lower panel, logarithmic scale) progressively increase with time. Model parameters: temperature=17.5 °C, max. algal growth: 1.0 d^{-1}, algal carrying capacity=0.2 mg C L^{-1}, lifespan=30 d.

with slightly changed initial values for one state variable, e.g. food concentration, the emerging dynamics progressively deviate from the original simulation (Fig. 6.4). Such an amplification of errors is a characteristic property of chaotic systems. In conclusion, it can be stated that the structured population model indeed shows a tendency to transient chaos (see Fig. 6.3 A & B).

In addition to the intrinsic potential of the model to display transient chaotic dynamics, a variable ambient temperature would likely force the chaotic behavior of the dynamics. Generally speaking, an application of this model to field populations will almost always result in complex transient dynamics and will potentially lead to chaotic behavior. Under field conditions, ambient temperature is highly dynamic due to variability within (seasonality) and between years and also due to pronounced vertical temperature gradients as usually prevailing in lakes and reservoirs of the temperate

region. Thus, it can be hypothesized that already minor changes in the temperature regime may induce considerable changes in the population dynamics of *Daphnia*. In fact, there is empirical evidence that *Daphnia* population dynamics are comparatively sensitive to temperature. For example, the timing of the spring clear water phase was found to be dependent on the temperature regime during early spring. This temperature regime is affected by the north atlantic oscillation (NAO), which consequently led to a synchronization of the clear water phases in many european lakes on a continental scale (SCHEFFER *et al.*, 2001; STRAILE, 2002). Furthermore, long-term investigations in Bautzen Reservoir showed that temperature conditions during winter and early spring potentially affect the population dynamics of *Daphnia* during summer (BENNDORF *et al.*, 2001). Interestingly, elevated temperatures in winter and early spring were often associated with a dramatic midsummer decline of the *Daphnia*-population later in the year. The mechanisms that mediate these developments were related to a faster population development early in the year leading to higher abundances in spring and, consequently, to an intensified resource overexploitation later on. This strong resource overexploitation led to a pronounced clear water phase with elevated non-consumptive mortality of *Daphnia*. A simultaneous occurrence of this non-consumptive mortality and predation by YOY fish in such warm years ultimately induced the observed midsummer decline of *Daphnia*. It was further pointed out that that observed population dynamics cannot be understood without focusing on population demography and its development over time (HÜLSMANN & WEILER, 2000; HÜLSMANN & VOIGT, 2002; HÜLSMANN, 2003), i.e. demographic effects have to be taken into account. Since temperature effects strongly interact with demographic effects (individual somatic growth and egg development are strongly controlled by temperature), detailed model simulations should support the hypothesis that elevated temperatures in early spring lead to a more pronounced resource overexploitation.

Simulations of a defined *Daphnia*-population at different temperatures have shown consumer resource dynamics to be strongly affected by ambient temperature (Fig. 6.5). Although equal initial values for daphnid abundance and biomass as well as for algal biomass have been applied, the emerging dynamics are clearly different from each other. The effect of increasing temperature does not simply lead to faster dynamics but also shifted the qualitative character of the consumer-resource dynamics. Most obviously, at the lower temperature the consumer-resource dynamics became more irregular and a prolonged transient phase occurred. In contrast to this, an elevated

temperature leads to cycles with an increased amplitude and, consequently, minimal *Daphnia* biomass were lower and thus closer to extinction. These results may indicate a destabilizing effect of elevated temperatures on the consumer resource dynamics of *Daphnia* and its algal prey. With respect to recent developments in the global climate and the ongoing tendency towards higher temperatures (IPCC, 2001) it appears to be an important issue of future investigations to clarify the extent of these temperature effects on plankton dynamics.

The factors causing the high sensitivity to ambient temperature are related to (i) different temperature scalings for algae and *Daphnia*, (ii) delaying effects within the life-cycle, and (iii) memory effects mediated by population demography. The latter factor is a characteristic property of structured populations since the population demography contains information about the population state in the past. In this example a lifespan of 30 days was applied, which means that events from the past 30 days can potentially affect the current state of the population and its dynamics.

However, in order to realize a more sophisticated test whether the model is capable to reproduce the temperature-driven processes observed by BENNDORF *et al.* (2001) it will be necessary to explicitly account for field conditions. This can only be achieved by including the model system into a community level model (see next section), e.g. in a water quality management model. Such models can account for the accompanying dynamics in phytoplankton succession, nutrient availability and top-down effects by predators.

6.3 Extensions of the model system

The presented model systems consist of an individual level model, including either empirical or mechanistic descriptions of relevant physiological processes, and an associated population level model allowing the simulation of population dynamics. Besides possible extensions that aim on introducing more detail into the existing model structure, e.g. introduction of diapause (individual level) or sexual reproduction (population level), it also appears useful to extend the model system by linking it to further levels of biological organization. Such extensions would be in line with the concept of a species-oriented approach and would, moreover, enhance and broaden its ability to combine existing knowledge. This section, therefore, pays attention to possible model extensions that lead to the inclusion of further levels of biological organization.

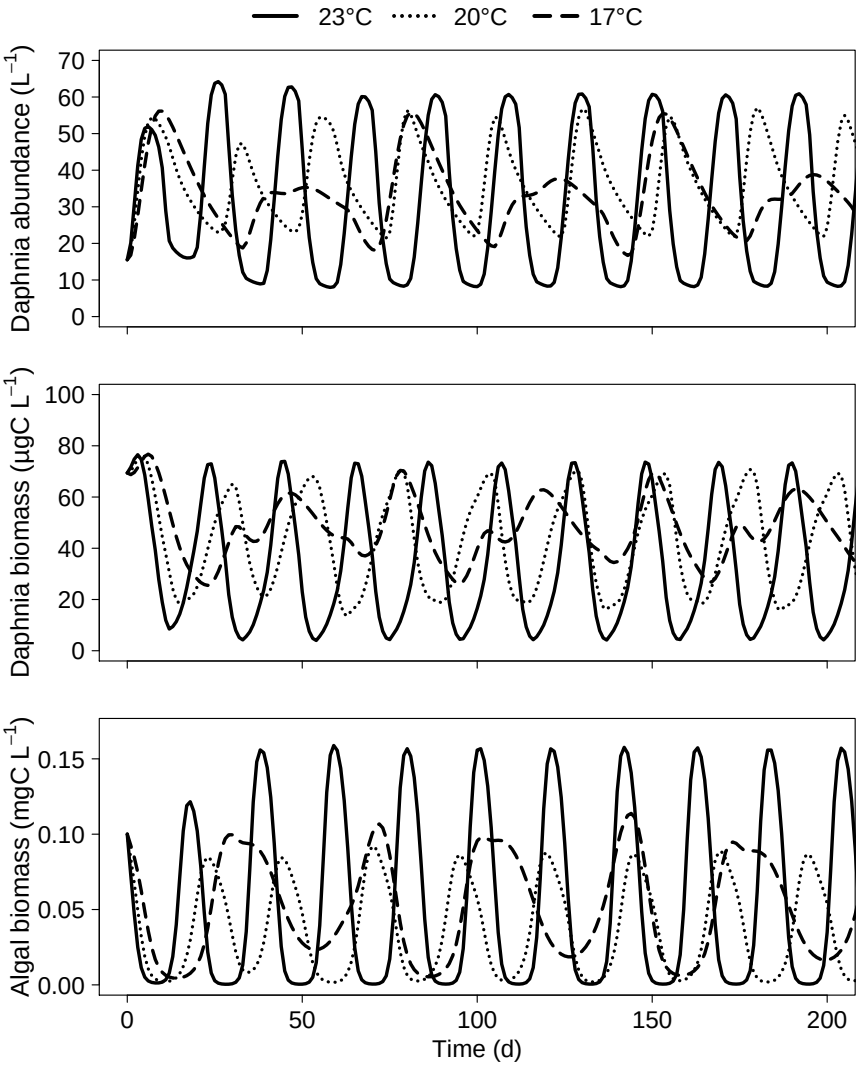

Figure 6.5: Transient dynamics for *Daphnia* abundance (upper panel), biomass (center) and algal biomass (lower panel) are plotted for three simulations at different temperatures (23 °C, 20 °C, 17 °C). Model parameters: max. algal growth at 20 °C: 1.0 d^{-1}, Arrhenius temperature for max. algal growth: 3378 K (according to ELLIOT *et al.*, 2000; REYNOLDS *et al.*, 2001), algal carrying capacity=0.2 mg C L^{-1}, lifespan=30 d.

6.3.1 Sub-individual level extensions

A mechanistic strategy to realize model extensions beneath the individual level would demand to focus on tissues, cells and, finally, genes. Although the necessity to bridge over all these hierarchical levels has already been recognized, a comprehensive understanding of the involved processes is still lacking (NISBET *et al.*, 2000). In comparison

to the well studied interactions between the individual level and the population level, for example, we have a rather incomplete picture about the interactions between genes, cells, and tissues — at least in terms of their implications within an ecological context. However, recent research on *Daphnia* provided evidence for important sub-individual level processes that potentially could be linked to a species-oriented model system.

Growth and individual ontogenesis does not only depend on ambient temperature and food quantity but also demands essential compounds in order to preserve homeostasis. *Daphnia* growth was shown to be potentially limited by the availability of phosphorus (stochiometric theory, see DEMOTT *et al.*, 1998; GAEDKE *et al.*, 2002; HESSEN *et al.*, 2005) or by essential organic compounds (poly-unsaturated fatty acids or sterols, see VON ELERT & WOLFFROM, 2001; MÜLLER-NAVARRA *et al.*, 2003; VON ELERT *et al.*, 2003). In order to account for these potential limiting factors it would be necessary to include such compounds in the chemical composition of the daphnids and their food. In fact, there are already model approaches available that take these details into account. A complex individual level model by HALLAM *et al.* (1990) allows to simulate the individual mass budget of fat, protein and carbohydrates for *Daphnia*. And a comparable approach by ANDERSON *et al.* (2005) focuses on the stoichiometric composition of *Daphnia* and its algal food with special emphasis on phosphorus. Both approaches indicate promising opportunities how the existing model system could be extended in order to account for these potential limiting nutritional compounds. An inclusion of these food quality effects on individual ontogenesis of *Daphnia* would be particularly interesting since this extended system will allow to investigate the emerging effects on the population level, which cannot be done with the existing models by HALLAM *et al.* (1990) and ANDERSON *et al.* (2005).

In this context it has to be emphasized that such extensions may require the introduction of a reserve compartment on the individual level since organisms show a certain potential to store essential nutrients. Carbon is usually stored in fat droplets in *Daphnia* (TESSIER & GOULDEN, 1982; TESSIER *et al.*, 1983) and nitrogen can be stored in proteins (GUISANDE & GLIWICZ, 1992). The capability of *Daphnia* to store phosphorus is certainly much lower, however, daphnid P-content was at least proven to be variable to some extent (DEMOTT *et al.*, 1998). According to the argumentation of KOOIJMAN (2001), all nutrients are firstly channelled into a reserve compartment from which they are distributed further into growth, reproduction and maintenance (for a more detailed description see also KOOIJMAN, 2000). Although

this is undoubtedly a defendable assumption, it appears problematic to parameterize the nutrient/energy flow from the reserves into further processes since empirical data about the relevant processes are still lacking.

Another attractive extension will be to link certain individual level traits to specific genetic markers. Although we do not yet have explicit information about the genetic control of a given trait it is obvious that observed traits can change over evolutionary time due to selection between competing genotypes (WEIDER, 1984; DE MEESTER *et al.*, 1995; SPAAK & RINGELBERG, 1997a; HAIRSTON *et al.*, 1999; DE MEESTER *et al.*, 2002). Fortunately, these evolutionary processes can be simulated without explicit information about the genetic basis by the application of genetic algorithms (e.g. GISKE *et al.*, 1998; HUSE *et al.*, 1999). Successful applications have proven the ability of these algorithms to simulate artificial evolution and they definitely provide a powerful tool to understand behavioral or life-history adaptations (SHERTZER & ELLNER, 2002; STRAND *et al.*, 2002). The application of genetic algorithms require the representation of a given trait in terms of a distinct parameter value (or a parameter combination), e.g. the value of κ as used in chapter 5 in order to represent a distinct resource allocation strategy. During the simulation, the value of this parameter of a given individual is inherited from its mother[1]. However, with a defined probability the parameter value of the offspring can be slightly modified by mutations. The survival probability of an individual depends on the respective phenotype of the trait and ambient environmental conditions, i.e. survival differs between genotypes. This enables selection of the best adapted genotype over time. On basis of individual based simulations such genetic algorithms can easily be introduced into the existing model system in order to enable a simulation of dynamic evolutionary processes. Of course, such modelling attempts would become even more powerful as soon as we know the relevant sub-individual level processes regulating a respective trait (e.g. the genetic control of κ).

6.3.2 Beyond the population level

In contrast to the limited knowledge available about the interplay between genetical and physiological processes, scientists have accumulated a broad body of mechanistical information about dynamics on the community and ecosystem level. Almost 20 years ago, limnologists started to give an axiomatic, process-oriented description

[1] or from its parents if non-parthenogenetic organisms are in the scope of the study

of the observed dynamics in lakes (SOMMER *et al.*, 1986). As mentioned in chapter 2, these information were also used for a quantitative description by developing dynamic models of whole lake ecosystems (e.g. BENNDORF & RECKNAGEL, 1982; HAMILTON & SCHLADOW, 1997; ARHONDITSIS & BRETT, 2005). Besides scientific purposes also economical reasons associated with water usage have motivated a relatively quick and diverse development of these water quality management models (WQM-models, see chapter 2). In order to expand the species-oriented model system to the community or ecosystem level it therefore appears promising to connect it to a WQM-model. Such a coupled model would include all necessary structures to account for the environmental complexity within the ecosystem and will enable an application to field situations. This will provide the opportunity to compare the outputs of the *Daphnia*-model with observed population dynamics in the field. As argued in chapter 2, a coupled model should solve existing problems in the zooplankton compartment of current WQM-models.

Such an inclusion would certainly increase the computational demand of a WQM-model considerably. For that reason the necessity may arise to change the architecture of the structured zooplankton model in order to increase the computational efficiency. In principle, there are two possible ways to realize this: (i) decrease the number of cohorts within the population by increasing the cohort width above 1 day (i.e. decrease demographic resolution), and (ii) decrease the spatial resolution of the WQM-model. However, such model changes will be associated with an aggregation error and it has to be carefully checked whether this error will cause unacceptable deviations.

Another consequence of including a structured population model of *Daphnia* spec. into a WQM-model will be that at least one further functional zooplankton group besides *Daphnia* is required. This is necessary, of course, since zooplankton communities of lakes are not always dominated by daphnids. For example, water bodies with a low trophic state are often dominated by calanoid copepods (e.g. MUCK & LAMPERT, 1984; MAIER, 1996; ADRIAN, 1997; KASPRZAK & KOSCHEL, 2000) whereas hypertrophic lakes with filamentous cyanobacteria are known to inhabit large populations of cyclopoid copepods or small-bodied cladoceran species (e.g. SOMMER *et al.*, 1986; MAIER, 1996; FULTON, 1988; KASPRZAK & KOSCHEL, 2000). Trophic interactions of these zooplankters can be diametrical to those known from daphnids (e.g. LYNCH, 1979; LAZZARO, 1987; SOMMER *et al.*, 2001; KAGAMI *et al.*, 2002). However, since grazing effects on the phytoplankton by copepods and small cladocerans

are normally less strong than those exerted by *Daphnia*, a simple solution of this problem may be sufficient. To implement just one further functional zooplankton group into the WQM-model, which may represent copepods, by using a standard population approach appears as being a good compromise between model complexity and a lifelike model structure.

An inclusion of this model system into a WQM-model will also induce dampening effects on the consumer-resource dynamics between *Daphnia* and its algal prey. On the one hand, detritus and components of the microbial loop (bacteria, protozoans) provide alternative food sources to *Daphnia*. In Bautzen Reservoir, KAMJUNKE *et al.* (1999) have shown that the microbial loop significantly contributed to the nutrition of *Daphnia* during the clear water phase. Detritus is mostly of poorer nutritional value (SAUNDERS, 1972; GULATI *et al.*, 2001) leading to lower assimilation efficiencies and slower growth. Such processes should weaken the non-consumptive mortality in the simulations during times with very low algal abundance. On the other hand, badly ingestible algae can interfere with *Daphnia* grazing (HORN, 1981; SOMMER *et al.*, 2001; LÜRLING & VAN DER GRINTEN, 2003) and, thus, reduce their ability to quickly exploit their resources. In conclusion, resource overexploitation by *Daphnia* should be less extreme than in the isolated system of *Daphnia* and one well ingestible algae (see Fig. 4.6). This dampening effects of detritus and badly ingestible algae can also be observed if consumer resource dynamics in mesocosms with *Daphnia* and well ingestible algae are compared with those dynamics observed in the pelagic zone of lakes (compare MCCAULEY & MURDOCH, 1987; MCCAULEY *et al.*, 1999).

From a scientific point of view a coupling of the existing species-oriented model system with a WQM-model would also be interesting since the emerging model would allow to investigate top-down effects within the food-web in more detail. By introducing an age- and size-structure in the population, a mechanistic simulation of size-selective predation by fish could be conducted and its consequences on lower trophic levels might be explored. Studies in the Bautzen reservoir showed that fish predation alone is not sufficient to explain the population breakdown of *Daphnia* (MEHNER *et al.*, 1998a; WAGNER *et al.*, 2004, e.g.). However, as soon as fish predation is not only viewed as a loss term on the population level but also its consequences on population demography are explicitly taken into account the picture may change. From simulation studies emerged that positive size selective predation by fish can have severe consequences on population dynamics of *Daphnia* by removing adult individuals

(MEHNER, 2000). Top-down effects by planktivorous fish are key mechanisms in the concept of biomanipulation (e.g. SHAPIRO & WRIGHT, 1984; BENNDORF, 1990; DEMELO *et al.*, 1992) and therefore of particular interest for scientific and applied purposes. In consequence, there is a strong need for ecosystem models that are capable of taking the relevant processes explicitly into account. This can be be achieved by an inclusion of the model system presented into a WQM-model.

7 Summary

The scope of this thesis was to develop a comprehensive model system of the genus *Daphnia*, a key organism in the pelagic food web of lakes and reservoirs and a widely used model organism in experimental and theoretical ecology. Although its central role in applied and basic research in aquatic ecology is obvious, there are still fundamental problems in modelling the observed dynamics of *Daphnia* (for details see chapter 2). Therefore, a basic motivation of this work was to use scientific results obtained in independently conducted research for developing a model that brings these results into context. Instead of following a 'problem-oriented' paradigm applicable to a single, well defined problem or scientific hypothesis, the underlying concept of the emerging model system was considered to be 'species-oriented'. Thus, various relevant processes are included into the framework in order to simulate the dynamics of daphnids displayed on different levels of biological organization. To facilitate its application to various problems in ecological research on the genus *Daphnia*, the model system fulfills the following three important properties:

- model outputs are thoroughly validated on experimental data in order to guarantee sound quantitative outputs of the model system
- the system spans over different levels of biological organization with special emphasis laid upon the individual level and the population level
- the model's architecture follows a nested design with a defined individual level model that is integrated into a population level model

The whole model system is able to describe an individual's development over time on basis of physiological properties of the organism and, furthermore, how these individual level processes interact with the dynamics on the population level. Due to its nested design, applications of separate submodels (e.g. the individual-level model) are possible.

Two different approaches have been realized in this thesis for achieving a species-orientated model of *Daphnia*. Firstly, an empirical model of growth and reproduction was developed on basis of a multiple regression model (chapter 3). This individual level model was applied within an individual based simulation in order to assign model outputs to the population level. Quantitative outputs of this empirical model were proven to be in accordance with experimental observations published by other authors (somatic growth: r^2 = 0.954, n = 88; egg production: r^2 = 0.898, n = 35). Ambient food concentration and temperature are input variables of the model. However, no density-dependent processes are incorporated, i.e. no feedback of daphnid grazing on its algal food can be simulated. The model can be applied to predict individual fitness and population growth under given environmental conditions. The applicability of the model has been documented by four simulation examples in chapter 3: (i) correlation between population growth rate and juvenile somatic growth rate, (ii) temperature scaling of population growth rate, (iii) food dependent size at first reproduction, and (iv) quantification of the costs of diel vertical migration of *Daphnia*. The model displayed plausible quantitative outputs over a broad range of temperatures ($2 \ldots 20^{\circ}$C) and food conditions ($0.1 \ldots 4$ mg C L^{-1}) and appeared to be well suited for computation intensive individual-based simulations, e.g. in spatial ecology. Due to its straightforward model architecture this model is easily transferable to other animal species.

Secondly, a mechanistic model of growth and reproduction of *Daphnia* based on energy allocation rules was developed (chapter 4). This bioenergetic approach, which follows the theory of dynamics energy budget models (DEB-models, KOOIJMAN, 2000), calculates individual somatic growth and egg production on basis of a closed carbon budget. It explicitly includes the quantitative description of physiological rates and thus provides an approach that links individual life-history to underlying physiological processes. Quantitative outputs have been validated on independent data from a life-table experiment of *Daphnia galeata*. For the first time, known so far to the author, an individual level model of *Daphnia* was validated to very low food concentrations close to minimal food requirements. Special physiological adaptations to low food conditions have been taken into account (reduced maintenance costs and improved assimilation efficiency). Such adaptations were well documented in experimental studies but, surprisingly, have not been regarded in modelling attempts so far. Outputs of the bioenergetic model were compared with predictions from another in-

dividual level model of *Daphnia* (Kooijman-Metz model, see KOOIJMAN & METZ, 1984), which neglects these special adaptations to food shortage. Simulation results showed that the Kooijmann-Metz model is not able to correctly predict individual life-history under very low food concentrations.

The bioenergetic model was further integrated into a structured population model in order to allow the simulation of population dynamics. This new population level model included density-dependent effects and enabled the simulation of consumer-resource dynamics. The emerging dynamics were shown to differ from those obtained from classical, unstructured population models. Reasons for these differences in the consumer-resource dynamics are straightforward: classical, unstructured models cannot account for demographic effects. Recently published detailed observations of *Daphnia* population dynamics in the Bautzen Reservoir (Germany) during spring and early summer have proven the importance of demographic effects in the field. These studies documented a number of consecutive events that were mirrored by simulations of the structured population model: (1) exponential growth during spring; (2) rapidly decreasing food concentrations (3) formation of a peak cohort at the end of the exponential growth phase (4) pronounced clear water phase as the consequence of resource overexploitation (5) *Daphnia* population suffers from starvation (6) increased non-consumptive mortality. It can be concluded that unstructured population models are not suited for simulating the dynamics of populations showing rapidly fluctuating demography as, for example, *Daphnia*.

In chapter 5, the model system was used to study resource allocation patterns and the adaptive value of life-history shifts of *Daphnia*. Since shifts in individual life-history imply a change in the underlying physiological processes the bioenergetic model from chapter 4 was applied for this purpose. Observed life-history shifts in response to fish kairomones can be reproduced by shifting the energy allocation towards increased investment into reproduction. This happens on the expense of energy allocation to somatic growth leading to slower growth. Life-history shifts of nine clones of *Daphnia galeata* $\times$ *hyalina*, measured in experiments of other authors, were used to parameterize the model. All clones showed a consistent response to fish kairomones by reducing the energy allocation towards growth and maintenance (reflected by the parameter κ). However, in six out of nine clones this shift was not sufficient to explain the observed life-histories. Additional energetic costs on the bioenergetic level have been detected in these clones when exposed to fish kairomones, which explains why

this life-history adaptation has evolved as an inducible defence. The adaptive value of the life-history shifts displayed by the nine clones was quantified by calculating population growth rates under a range of possible positive size-selective predation regimes. All observed life-history shifts appeared to be adaptive. However, clones having high additional costs on the bioenergetic level realized an adaptive value of their life-history shift only under very intense predation. As far as known to the author, this is the first study that puts resource allocation, energetic costs and adaptive value of predator induced life-history shifts - using empirical data - into one theoretical framework.

In conclusion, the species oriented model system presented in this thesis can contribute to our understanding of observed individual and population level dynamics of *Daphnia*. The model structure is well documented and outputs are plausible and thoroughly validated. Due to its nested design the model system is easily expandable and can be coupled to other models with relatively low efforts (e.g. integration into water quality management models). This system opens a broad field of future model applications in basic and applied research related to *Daphnia*.

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10 List of publications

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